1976

Plant Demographic Studies of Desert Annual Communities in Northern Utah Dominated by Non-Native Weedy Species

D.R. Duba

B.E. Norton

1974/75 PROGRESS REPORT

PLANT DEMOGRAPHIC STUDIES OF DESERT ANNUAL COMMUNITIES IN NORTHERN UTAH DOMINATED BY NON-NATIVE WEEDY SPECIES

D. R. Duba and B. E. Norton
Utah State University

US/IBP DESERT BIOME
RESEARCH MEMORANDUM 76-13

in

REPORTS OF 1975 PROGRESS
Volume 3: Process Studies
Plant Section, pp. 67-102

1975 Proposal No. 2.3.1.9

Printed 1976

Ecology Center, Utah State University, Logan, Utah 84322

ABSTRACT

Field and laboratory investigations were conducted relating to factors controlling distribution and abundance of annual species growing in a disturbed portion of the salt desert shrub zone on fine-textured soils. Dominant species on the site in the two study years were the nonnative, halophytic, late-summer-maturing, *Halogeton glomeratus* (Bieb.) C.A. Mey. and *Bassia hyssopifolia* (Pall.) Kuntze. Contrasting amounts of precipitation were received in the two years; in 1974, spring conditions were so dry that two early-maturing, subdominant annuals, *Descurainia pinnata* (Walt.) Britton and *Lepidium perfoliatum* L., were essentially absent. They successfully reproduced under more favorable 1975 conditions. Studies on species distribution centered around factors responsible for occurrence of large (20-30 m across), adjacent, essentially pure stands of *Bassia* and *Halogeton*. It was determined that few seeds dispersed more than 1 or 2 m from parent plants; and that seedling establishment success of the species was significantly different in the two vegetation types, commensurate with soil surface physical and chemical differences. The less drought-tolerant *Bassia* was confined to soils which had higher water potential in summer than the areas occupied by the succulent *Halogeton*. *Bassia* responded with more rapid growth when water availability increased and suppressed *Halogeton* in both of the growth-chamber competition studies. The adjacent pure communities are believed to be maintained by *Bassia's* inability to establish on soils dominated by *Halogeton* and by *Bassia's* competitive superiority when both species become established together. Studies on plant abundance involved making quantitative estimates of numbers of seeds or plants per unit area in different life cycle phases during the study period. The objective of these studies was to determine the manner in which each year's seed production was utilized (in terms of dormancy of seeds in soil, germination, mortality or reproduction). It was determined that residence time of seeds in soil was short, since seeds germinated freely after overwintering. Consequently, the vegetation composition was closely related to the previous year's seed production. Tremendous mortality takes place during the seedling establishment phase, as only 8% of seeds sown into marked quadrats survived until mid-May. Mortality during summer was highly density-dependent. Plant plasticity served a homeostatic function on one site which suffered a seed crop failure in 1974. The few plants established there in 1975 became very large so that total seed production was not greatly different from areas which had a substantial amount of seed production in 1974.

INTRODUCTION

An inadvertent, but inevitable, result of European man's settlement of the western United States was the introduction of several species of weedy, highly competitive, nonnative annual plants. The settlers' livestock abused the native vegetation on vast areas of these semiarid rangelands by overgrazing. Intensity of grazing was so high in many areas that the fragile shrub-steppe plant associations were unable to regenerate, often allowing the opportunistic weedy annuals to become dominant on these sites.

This investigation was undertaken to discover some of the major factors controlling plant species distribution and abundance in a community composed mainly of nonnative annual plants in a disturbed area of the sagebrush steppe zone in northern Utah. The studies were carried out in 1974 and 1975 on a community composed almost entirely of annual plants. The dominant species in this community were two late-summer-flowering nonnative species: *Halogeton glomeratus* (Bieb.) C. A. Mey. and *Bassia hyssopifolia* (Pall.) Kuntze., both in the family Chenopodiaceae. Two subdominant, late-spring-flowering members of the Cruciferae, tansy mustard [*Descurainia pinnata* (Walt.) Britton], the only indigenous species, and yellowflower pepperweed (*Lepidium perfoliatum* L.), were present in 1975. Investigations of their ecology primarily attempted to answer two sorts of questions: what were the major factors influencing distributions of the two species from point to point on the study site, and what were the major factors influencing their abundance from one year to another. The hope was that by studying the population behavior of these species, some insights into the ecology of desert annual plants in general might be realized.

All field work was conducted on the south Curlew Valley Validation Site of the U.S. International Biological Program, Desert Biome. The site is located in Box Elder County, northern Utah, approximately 25 km southwest of Snowville, in sections 5-8 of township 13 North, Range 9 West at 1320 m elevation (Balph et al. 1973). In the summer of 1973 the site and some surrounding terrain, several square kilometers in all, was fenced to prevent livestock from disturbing any of the ongoing studies.

In most areas of the site, the soil surface exhibits two features which are of importance in the establishment of annual plants. The high silt and clay fractions cause the soil to shrink and swell, dependent on its water content. This phenomenon has resulted in the development of polygonally shaped surface peds, roughly 10-20 cm across, which are separated by narrow cracks from 2-5 cm in depth. The other feature has been referred to as a vesicular layer (Blackburn and Skau 1974; Hugie and Passey 1964); the peds frequently display a moderate platy structure interlayered with thousands of tiny, gas-containing vesicles that leaven the soil, giving it a structural appearance similar to a piece of bread. These vesicles increase the porosity of the soil surface, making it effectively drier (due to the gas-containing spaces) and

softer (due to the compressibility of the layer). The relationships of these soil properties to annual plant establishment will be discussed later.

In May 1974, four areas in the validation site were selected for investigation, each area approximately 25 m^2. All four of the plots are located in the southwest part of the fenced site and are situated within an area approximately ½ km long x ¼ km wide.

The first site (subsequently referred to as "hill site"), on which the majority of the investigation was done, exhibits an abrupt boundary between nearly pure stands of *Bassia* and *Halogeton*. The ecotone occurs over a distance of less than 2.5 m and corresponds with a gentle, and scarcely perceptible, undulation in the topography. The *Halogeton* is found on the higher ground and *Bassia* is in the depression some 20 to 70 cm lower.

The second site, located near one of the fenced boundaries (and subsequently referred to as "fence site"), is similar in most respects to the hill site, except that the separation of *Bassia* and *Halogeton* communities is not associated with topographic relief.

The third site (subsequently referred to as "sage site") was chosen to include an isolated group of sagebrush plants which occurred in this annual area. The eastern one-third of the site is a somewhat open stand of mature sagebrush plants, about 30 in all, while the western half is almost exclusively *Halogeton*. *Lepidium* is scattered between the sagebrush clumps and extends into the open ground away from the sagebrush. This was almost the only place were *Lepidium* occurred as the dominant annual species.

The fourth site (subsequently referred to as "bare site") had the highest density of *Sitanion*, but seemed to have a lower annual plant density when first observed in spring 1974. *Bassia* and *Halogeton* were both present here in fairly equal numbers but did not exhibit the negative association so evident on the first two sites.

These four sites served different roles in fulfilling the study objectives. The sage and bare sites were not particularly useful in investigating the causes responsible for adjacent pure stands of *Bassia* and *Halogeton*, because they did not display the phenomenon. Rather, the hill and fence sites were the major sources of information on this topic. All four sites contributed to the quantitative seed budget portion of the study.

Data for this report are stored under DSCODES A3UDD01, 02.

OBJECTIVES

The objectives of the study were twofold:

1. To investigate possible factors responsible for occurrence of adjacent, essentially pure, stands of *Bassia* and *Halogeton* in the field. The assumption here is that since the pure stands were so proximitous, they should have been invaded by the absent species. This problem was studied in relation to seed germinability and dispersal, seedling establishment, soil differences, plant drought tolerance and competititive interactions between the species.
2. To gain insights on the relative importance of dormancy, mortality or reproduction in controlling the dynamics of these annual communities. By estimating densities of seeds or plants present in different stages of the life cycle, the critical periods controlling plant numbers can be investigated. Since the community is generated anew each year from seed, its trend hinges on the manner in which each year's seed production is dissipated. Whether the seed remains dormant in the soil, germinates and dies, or successfully reproduces -- and the amount of seed produced -- are the critical factors determining vegetation composition.

METHODS

Bassia-Halogeton Comparative Studies

Density at Fixed Points

After the four plots were selected, their boundaries were defined by driving painted, wooden dowel stakes into the ground at 5 x 5 m intervals to form a rectangular grid of stakes. Plots were oriented with their axes in generally NS and EW directions. Three of the plots were 25 x 20 m while the hill plot was 30 x 25 m.

These stakes were to be used for general orientation as well as for repeated sampling of plant densities. With the latter in mind, as the stakes were being located, any position which constituted an irregularity for data collection (such as the base of a sagebrush plant) was moved 50 cm to one side of the grid intersection so that sampling could be confined to vegetation of uniform physiognomy within the area. About 5-8% of the stakes were relocated in this fashion.

Density counts of numbers of individuals by species were made at each of these posts on June 24 and September 14, 1974, and in 1975 up to six times between May 26 and August 31. The sampling device was, in all cases, a 10 x 10 cm rigid wire frame placed in the northwest quadrant of each stake, with the stake itself serving as the southeastern corner of the quadrat. At the first sample period, a small wire marker was pushed into the soil at the northwestern corner of the quadrat, enabling replicated sampling of fixed quadrats by aligning diagonal corners of the frame with the wooden stake and the wire.

Seed Dispersal Experiment

During the period of seed dissemination in 1974 an experiment was conducted on the hill study area to get an idea of how far *Bassia* and *Halogeton* seeds moved from parent plants, and to estimate the proportion of the two kinds of seeds entering the different vegetation types from the 1974

seed crop. On August 28, before seeds had begun to fall, 60 metal plates, each 10 x 15 cm in size, were placed on the plot in three rows, 20 plates per row. One row consisted of plates scattered at more or less equal distances along the boundary between *Bassia* and *Halogeton* while the other two rows were parallel to the first but placed 3 m on either side of it, one in *Bassia* and the other in *Halogeton* vegetation. Each plate was fixed to the ground with two pieces of stiff wire.

The upper surface of each plate was coated with a thin layer of Tanglefoot (manufactured by Tanglefoot Company), a very sticky, commercially prepared substance designed to catch insects. It served equally well to catch seeds in this experiment and in a similar one conducted by Knipe and Springfield (1972) in New Mexico. As the season progressed and seeds began to fall from plants, they appeared on the sticky plates lying beneath the canopy. At intervals of one or two weeks until November 17, plates which had accumulated many seeds were replaced with clean ones, while plates with few seeds remained in the field. Numbers and kinds of seeds on each plate were recorded in the laboratory.

Seed Germination in Relation to Water Potential

The ability of seeds to germinate under a range of water potentials was considered to be important to establishment of plants in the field and was tested in the laboratory using sodium chloride (ionic) and polyethylene glycol (nonionic) solutions. All solutions were mixed from a .01 molal calcium chloride stock solution as calcium has been found to have a germination-enhancing effect (Chaudhuri and Wiebe 1968) and is ever-present in Curlew Valley soils. Solutions were $CaCl_2$ stock only (0.5 bar), or were mixed and adjusted to 5, 10, 15 and 20 bars with a thermocouple psychrometer-microvoltmeter apparatus. Each petri dish contained 50 *Bassia* or *Halogeton* seeds and 20 ml of the appropriate solution. There were five replicates for each treatment for each species, making a total of 90 dishes. They were randomly arranged in a growth chamber and maintained at 20 C in the dark except for two brief periods to check the progress of germination.

The seed was considered germinated when the radicle was more than 3 mm long. Germinated seeds were tallied and removed from dishes at 63 and 97 hr after being placed in the solutions.

Seedling Establishment Experiment

Another field experiment was designed to investigate the establishment success of the two species in different vegetation types and on the different study areas. A secondary aspect was to see if treating seeds with Captan powder (a fungicide) would affect their establishment success.

In August 1974, small cardboard boxes (about 20 x 30 x 5 cm) were placed at random over patches of soil in the different areas. They served to exclose seeds dispersing from the 1974 seed crop and, later in the year, the covered plots became receptacles for experimental seeds sown onto the soil. A total of 75 boxes was placed in the field, distributed as follows: 20 each on the hill and fence sites, with 10 in each of the two vegetation types; 20 in the sagebrush site, with 10 in the open community away from the sagebrush and 10 at the perimeter of sagebrush canopies; 15 scattered over the bare site.

These boxes remained in place until December 20, at which time the boxes were removed and lots of 200 seeds were sown onto marked 1-dm^2 quadrats. Each lot contained 100 *Bassia* and 100 black *Halogeton* seeds. Every box received one lot of seeds except for those on the hill site, which received two. The additional treatment on this site was seed which had been coated with Captan. Seeds were scattered evenly within the bounds of the 1-dm^2 quadrats and a small amount of water ($\sim$25 ml) was poured over it, care being taken to prevent seeds from washing out of the quadrat. At the time seeds were sown, the ground was frozen, so the water soon turned to ice, fixing the seeds on the quadrat. Finally, the quadrat was covered with snow to further diminish the possibility of seed movement. The following spring, on May 16, the quadrats were censused for numbers of established plants.

Drought Tolerance Experiment

An aspect of the ecology of *Bassia and Halogeton* which was considered important to their distribution on the study site was their relative ability to withstand drought. This investigation, patterned after one done by Pemadasa and Lovell (1974) was done in the greenhouse during September and October 1975, using plants grown in pots. It involved growing plants for a short time with an adequate water supply, then letting the pots dry out to a predetermined water content, followed by watering and observation of the number of plants surviving the drought treatment.

On August 31, 32 Styrofoam pots, 15 cm in diameter and 12 cm tall, were weighed and to each was added, in order, without mixing, the following: 80 g gravel, 1200 g Thiokol silt loam soil (collected where both species grew), 150 g greenhouse potting soil and 12 g vermiculite, all at oven-dry condition. Before the vermiculite was added, enough *Bassia* or *Halogeton* seeds were sown to establish 25 plants per pot. All pots were kept saturated for several days by sitting in large, water-containing pans in the greenhouse. The *Bassia* plants established well but the *Halogeton* did not, possibly due to the warm (28-32 C) temperatures in the greenhouse. *Halogeton* seeds were sown again but the plants were kept in the growth chamber at cool temperatures (15 C day, 8 C night) for about a week.

The 16 pots were divided into three treatment groups, differing in severity of drought, and an undroughted control maintained at 15-20% soil water content. Since the weights of the soils and pots were known, it was possible to compute the weight of a pot at a given soil water content. The three treatments were dried to increasingly low levels of soil water content, which took from 10 to 20 days after they dropped

below the 20% level at which the controls were maintained. After the drought was ended, each pot was returned to the control water content for an additional two weeks, harvested and dry weight of stems determined.

Soil Analyses

Soil sampling and profile descriptions—Samples of soil for several quantitative analyses were collected from two locations in both *Bassia* and *Halogeton* vegetation types of the hill site in September 1975. Soil was collected from the surface 3 cm and at 14-15 and 29-30 cm for each point. Analyses were done by the Soil, Plant and Water Analysis Laboratory at Utah State. Four bulk density measurements to a 5-cm depth were taken in each vegetation type of the hill plot using a metal ring. A soil profile was described in both vegetation types.

Psychrometric measurements of soil water potential—In the first part of June 1975, a total of 24 Wescor (Wescor, Inc., Logan, Utah) thermocouple psychrometers were installed at 4- and 12-cm depths on the hill plot to investigate water availability in the two vegetation types. At the 4-cm depth, pairs of psychrometers were installed with one member under the center of a polygonal soil ped and its companion at the base of one of the cracks adjacent to the ped. The distance between a psychrometer and its mate averaged 5-7 cm. Eight of these pairs were installed, four in each vegetation type, and readings were taken on them at bihourly intervals from 6 a.m. to 8 p.m., but starting at 2 p.m. on June 20 and ending at noon on June 24. An S-B Systems microvoltmeter was used for taking the readings. Commencement of sampling coincided with the occurrence of a fairly substantial rainstorm ($\sim$15 mm) followed by several days of warm weather which dried out the soil.

At the 12-cm depth, eight psychrometers were installed, four in each vegetation type, and readings were taken at irregular intervals until August 5.

After completion of sampling, all psychrometers were dug up and calibrated using 0.1, 0.5, 1.0 and 1.5 molal sodium chloride solutions. Graphs of water potential vs. microvolt output were drawn for each psychrometer. Field microvolt readings, corrected to 25 C, were converted to water potential using these calibration curves (Brown 1970).

Photo comparisons of soil peds—In the fall of 1974, 10 small areas (approximately 50 x 50 cm) which exhibited particularly evident development of polygonal soil ped structure, were marked and photographed to record the positions of the cracks between soil peds. In fall 1975, these same areas were again photographed to allow comparisons between the two years to see if changes had taken place in the positions of cracks or the shape of surface peds. If cracks closed during the winter wet period, and reopened along different lines on drying, many seeds might become buried at the base of the closed cracks (about 4 cm deep) and would be unlikely to emerge on germination. The slides from the two years were projected side by side to allow visual comparison and sketching of the location of cracks.

Competition Experiments

Field watering of plants—On the fence site in June 1974, 22 points were selected and marked along the *Bassia-Halogeton* ecotone to conduct an experiment on the effect of watering on plant survival and dry weight biomass. In selecting points for the study, an effort was made to find areas which contained approximately equal numbers of *Bassia* and *Halogeton*. On June 26, density counts were made at each point in two different quadrants, again using the 10 x 10 cm frame. After this initial count, half of the plots received 25 mm of "rain," applied using a large can with holes in the bottom and confined to the experimental area by a circular, metal collar 40 cm in diameter, which was pressed 4 cm into the soil to prevent lateral flow of water. This treatment was repeated weekly through the summer to half the plots, while the others received no water. Some adverse effects occurred to watered plants; soil erosion took place during water application, causing occasional stems, particularly of *Bassia*, to bend over and become mud-covered. This disturbance may have been detrimental to plant growth.

Density counts were made at approximately biweekly intervals on the fixed sampling quadrats, accompanied, beginning July 23, by harvests of above- and below-ground portions of plant material from two of the watered quadrats per sample period. Plants from the control quadrats were not harvested so that density counts on them could be continued; adjoining areas of unwatered vegetation were harvested to serve as biomass controls for the watered plants.

Harvesting was done using a shovel, first loosening the soil all around the selected quadrat to a depth of about 30 cm and then carefully loosening the soil within the plot and removing the plants so as to maximize the length of root collected. Roots harvested were seldom more than 15-20 cm in length, since by this depth they had become so fine ($<$1 mm diamter) that they broke easily. In the laboratory, plants were carefully washed to remove all dirt, dried in an oven for approximately 72 hr at 42 C and then weighed to the nearest milligram. At each sample date 30 plants of each species from the watered and unwatered conditions were randomly selected and weighed.

Growth chamber studies—Two separate competition experiments were done with *Bassia* and *Halogeton* based on general experimental designs of Harper (1960, 1961) and deWit (1960) using growth chambers and plants grown in pots. Seed for these experiments was obtained from the Curlew Valley site by collecting whole plants retaining seed in September 1974. These were stored outdoors in a dry place for several months and were then gently broken up and put through sieves to separate seeds from other plant material.

Preliminary germination trials done at this time showed that a high percentage of *Bassia* seeds germinated but only about 60% of *Halogeton* black seeds would germinate. Consequently, they were given a stratification treatment, successfully used by Cronin (1973), which amounted to

placing the seeds in water for a few hours, allowing imbibition, and then freezing them for a period of four weeks or more. *Halogeton* black seeds were frozen for 2½ months, whereupon several hundred were thawed and germinated in petri dishes containing water, yielding nearly 95% germination within 48 hr.

The next procedure was to establish the seedlings successfully on soil from Curlew Valley. This proved to be a serious problem due to the high silt content of the Thiokol silt loam (Balph et al. 1973) and the soil surface structure. This fragile, highly aerated surface crust structure is destroyed when the soil is disturbed. When placed in pots and wetted, the soil surface becomes so hard that seeds sown on it cannot send their roots downward, while seeds sown slightly below the surface do not emerge in large numbers.

As a result of this problem, several different soil surface amendments were tried in order to obtain a greater percent emergence of sown seeds. These trials were done using enough seeds and pots to get a rough idea of the emergence percentage for the two species. Seeds were usually soaked in water for about 12 hr before sowing to permit imbibition. Soil in the pots was generally water-saturated and maintained that way for several days after seed sowing. Some of the treatments included sowing seed on the soil surface or about ½ cm below the surface, making microfurrows on the surface before sowing seed, pressing each seed slightly down beneath the surface, or covering the Thiokol soil with a thin layer of peat moss or a potting soil mixture.

The arrangement that worked best involved placing a thin layer of a loamy potting soil mixture over the Thiokol soil, sowing the seeds atop this, and covering them with a 5-mm layer of vermiculite. This regimen gave emergence of 70-80% for *Bassia* and 65-75% for *Halogeton*. Unfortunately, this technique was not discovered before the first growth chamber study began, but it made satisfactory establishment of plants possible in subsequent studies.

Timing-proportions study—The first growth chamber study was designed to test several factors which might be important in the competitive relations between these two species. Plants were grown in pots, each pot containing 36 individuals, but the treatments had different proportions of species, as follows: 0:1, ⅓:⅔, ½:½, ⅔:⅓, 1:0. The other experimental factor was the time at which seeds of the two species were sown into the mixed pots; both seed species were sown either at the same time or one species was sown eight days earlier or later than the other. Thus there were three timing treatments for the mixed pots and five stand proportions, each treatment replicated four times in a completely randomized factorial design, making a total of 44 pots.

Each pot was 10 x 10 cm and 15 cm tall. The following substances were added in order: 15 g vermiculite, 733 g Thiokol soil (collected at a point where both species were growing) and 85 g of a potting soil mix. Soils had been oven-dried at 110 C for several days. *Halogeton* seeds were thawed and each seed for every pot was gently pressed slightly into the soil surface; dry *Bassia* seeds were scattered evenly on the soil surface. All pots were placed in a large, water-filled pan overnight to allow the soil to become saturated. Initially, 24 pots were sown with only one kind of seed, half receiving *Halogeton* and half *Bassia;* eight days later the other species was sown into the appropriate mixed pot to implement the timing aspect of the study. When these seeds were sown, the pots were also resaturated to make water available for imbibition. The soil surface was kept damp during seedling establishment by wetting it with a spray bottle periodically.

All pots were transferred to a Sherer-Gillette growth chamber after the initial overnight soak. The experimental pots were randomly arranged in a rectangular pattern and were enclosed by a buffering perimeter of nonexperimental pots so that all experimentals were surrounded by four other pots. Every few days the pots were removed from the chamber and replaced in a random order so as to minimize any effects due to differences in temperature or light intensity from point to point within the growth chamber.

At the start of the experiment, 16 new, 40-watt fluorescent tubes were installed in the chamber along with four 75-watt and four 150-watt incandescent light bulbs. Light intensity in the chamber ranged from 766 to 894 μeinsteins$\cdot m^{-2}\cdot s^{-1}$ (between 400-700 nm) at the soil surface on June 6, 1975, as measured by a quantum sensor (Biggs et al. 1971). An outdoor reading taken on a cloudless summer day would be about 2000 μ einsteins. Spectroradiometric readings were also taken in the ultraviolet radiation range from 280-400 nm (see Appendix I).

Photoperiod in the growth chamber was initially set to correspond to a mid-April daylength with incandescent lights coming on about 15 min earlier and shutting of about 15 min later than the fluorescent tubes. Every few days the daylength was changed, in correspondence with the natural seasonal progression. Temperatures were set using daily averages of bihourly temperature records from the Curlew Valley site for 1974. Slight adjustments in growth chamber temperature were sometimes made daily but more often were made every three or four days. The growth chamber was designed such that no temperature fluctuations would occur within the period of a temperature setting. Day and night temperatures were constant over their respective time periods, which is a departure from the continuous temperature variation in nature. The growth chamber was unable to maintain night temperatures below 2 C or day temperatures below 13 C, so that during the initial weeks of the experiment, temperatures were sometimes 5-7 C warmer than in the field.

Seeds were sown into the pots on May 12, 1975, with the late seeds being added on May 20. The pots were allowed to dry out until they dropped below a soil water content of 20% by weight, at which time they were restored to 20%

water content by adding water. For most pots, watering began on about June 1, with weights being checked every other day and water replenished as needed.

By the end of June, it was decided to increase the amount of water added to each pot to compensate for weight of plant material that had grown in the pot, so that soil water content would not be underestimated. Plants were collected from the field and their stem length and fresh weight determined. This enabled plotting an approximate relation between height and fresh weight. Average heights of plants in pots were measured and the increase in water requirement computed, varying from 4-12 g for the different treatments. On July 24 this compensation was increased, allowing for continued plant growth, and varied from 5-15 g. This adjustment amounted to 15-20% of the water added at each time period.

On July 14 the soil water content was decreased from 20 to 17%, reflecting the increasing dryness plants experience in the field. Beginning August 5, water additions were made every day since plants were large enough to rapidly transpire each day's addition, causing occasional wilting of *Bassia*.

On September 9, all plants were harvested; stems were clipped at ground level, oven-dried at 45 C for three days and weighed. Roots were washed from the soil by first removing the soil block from the pot, soaking it in water and then loosening the soil away from the root mass. A series of rinses and sieves was used to remove as much soil as possible from the roots. All roots from each pot were placed in a bag, dried and weighed. It was impossible to distinguish *Bassia* roots from *Halogeton* roots based on any microscopic observation; their separation would have been impossible due to the large number of intertwined roots.

Soil-watering levels study—The second growth chamber study was quite similar to the first but different experimental factors were investigated. Two different soils from the hill site were used, in which either *Bassia* or *Halogeton* grew nearly exclusively. Pots were maintained at different soil water contents of 12, 18 or 24% by weight. All pots contained 36 plants in either pure or mixed stands; the mixed pots contained 18 of each species. Thus, the different treatments were two soil types, three watering levels and three stand types, each treatment combination replicated four times making a total of 72 pots in a completely randomized factorial design.

Procedural differences from the first experiment were few. A 5-mm layer of vermiculite was used to cover the loam soil after the seeds had been sown. Seeds were sown October 1 and plants were harvested November 26, as differences between treatments were evident at that time. No additional increment of water was added to compensate for the weight of plants in the pots. Roots were not harvested. In all other respects, procedures were the same as in the first study.

Seed Buget-Life Cycle Studies

Field Germinability of Seeds.

On December 20, 1974, 24 small packets of seeds were buried at 1- and 3-cm depths in the two different vegetation types on the hill site. Packets were 5 x 5 cm in size and made of finely woven Saran, with a mesh of about .6 mm so that seeds could not fall out. Each packet contained 100 seeds of either *Bassia* or *Halogeton* and approximately 20 cc of fine-textured, seed-free soil. In the field the frozen ground was wetted, causing it to soften so that it could be dug and the packets buried. In each vegetation type there were three replicates of each of the species at both depths. In the process of burying the seeds, the soil surface structure was destroyed so that none of the germinated seeds was able to emerge; however, the packets were dug up the following May and the contents examined for seeds which had failed to germinate.

Soil Seed Reserves

In July of 1974 and 1975, samples of the soil were collected from the sites and were examined for the numbers of seeds of annual plant species present. Germination had been completed for the current season. The sampling device was a metal frame 1 dm^2 by 3 cm high; it was pressed into the soil to the 3-cm depth, and a shovel was used to remove the sampler and some surrounding soil. A metal plate was forced along the bottom edge of the sampler leaving a soil block of 300 cc which was dumped into a bag.

In 1974, 80 samples were collected, 20 from each site. On the hill and fence sites, two transects of 10 samples each were taken across the ecotone, the sample points spaced 1 m apart with the middle of the transect at the boundary between the vegetation types. On the sagebrush site, 10 samples were taken in the open, away from the sagebrush; the other 10 samples were taken within the sagebrush-dominated vegetation. The samples from the bare site were randomly scattered.

In 1975, only 35 samples were taken and the bare site was not sampled. On the hill and fence sites, seven samples were randomly collected within eacch vegetation type, making a total of 28 samples, while the other seven were from the sagebrush-dominated vegetation on the sagebrush site. The sampling was scaled down because of the labor-intensive and time-consuming work in processing and analyzing each sample.

In the laboratory, all samples were processed in the same way. First, any large stems or pieces of plant material were removed from the soil and the soil was placed on a large (30 x 30 cm) piece of fine mesh organdy cloth, the corners drawn up and tied, enclosing the soil. Next, the bag was placed in a large pan of water and allowed to soak for several minutes. The bag was then gently squeezed and washed, breaking up the soil aggregates and allowing particles smaller than the bag mesh size (clay and silt particles) to settle out. This washing and rinsing continued

through several changes of water until soil no longer sifted out. The remains of the sample were finally washed onto a large piece of filter paper in a Buchner funnel, excess water was removed with suction, the filter paper removed from the funnel and the sample placed in a drying oven at 37 C for several days.

Dried samples were dumped into a #40 soil sieve and shaken for a few minutes. The fine fraction passing through the sieve was discarded, as it had been determined that the smallest seeds would not pass through, while that retained on the sieve was divided into the two equal portions and one of these examined under low magnification with a dissecting microscope. The different species of seeds were easily recognizable; those that were whole and hard were assumed to be viable (Stoller and Wax 1974), and were removed with a tweezers and counted. The microscopic examination of the samples proved to be very tedious; ultimately several hundred hours were spent on this phase of the study.

Plant Establishment from Seed in Summer

Beginning on July 17, 1974, a number of quadrats, 50 x 25 cm, were watered weekly with a watering can to see if there was a remnant of germinable seed left from the spring pullulation which would respond to summer moisture. Each plot received the equivalent of 25 mm of "rainfall" per week. Water was confined to the plots using metal frames (60 x 35 cm) which were pressed into the soil and which prevented water from running laterally off the plot. Prior to beginning the watering experiment, all live vegetation was removed from each plot so that newly emergent plants could be noticed. They, in turn, were removed each week.

The hill and fence sites each had a total of 30 pairs of plots, 10 pairs in each vegetation type and 10 along the ecotone. The sagebrush area had 14 pairs of plots, seven in the open and seven in the sagebrush-dominated vegetation. The bare site had 12 pairs scattered randomly over the plot.

During the final two weeks of supplemental watering (September 1-14), the amount added was doubled on 35 plots by supplying 25 mm on a semiweekly basis.

Seed Exclosures

The watered plots described above were used along with the previously mentioned covered plots (into which seed was sown) to conduct a study on the effect of exclosure of 1974 fall seed production on the density and composition of 1975 vegetation. One-half of the watered plots were covered with cardboard boxes in mid-September 1974. These boxes, which were slightly larger than the plot, were pushed down securely into the soil and rocks were placed on top of them so they could not be blown away. They stayed in place until January 1975 -- long after fall seed dispersal had ceased -- when they were removed. By this time, the ground was frozen and snow-covered so that no movement of seeds would take place.

The different plots served different purposes in this experiment. The watered, covered plots had no seed input from 1974, so that only seed dating from 1973 or earlier could generate plants for the 1975 community, while the watered, uncovered plots received a natural allotment of the 1974 seed crop. The difference between these treatments would provide an estimate of the contribution to the 1975 vegetation from 1974 seed. Similarly, a difference between covered, unwatered and covered, watered plots would be due to the water applied in 1974. Covered and uncovered watered plots were adjacent to each other and observed in pairs, so as to minimize differences from point to point within the four areas.

On May 26, 1975, density counts were taken of the number of individuals established in the various plots. Each of the watered plots was large enough to accommodate three 1-dm^2 subsamples within the plot, while the unwatered plots had enough space for only one 1-dm^2 sample. The subsample boundaries were marked and censused at approximately biweekly intervals through the 1975 growing season.

Seed Production

In order to make precise estimates of the numbers of seeds produced on the different areas, numerous whole plants were harvested in 1974 and 1975 when seeds were maturing on the plants. In mid-September of both years, *Bassia* and *Halogeton* plants were sampled while *Descurainia* and *Lepidium*, not present in 1974, were sampled only in early July of 1975. The permanent stakes on the areas were used as sampling points, from two to four samples being taken at points 1 m from each stake in the cardinal compass directions. Each sample quadrat was 1 dm^2; all plants inside the plot were removed and placed in a bag. The number of points sampled was not the same among the different areas, since some were less densely vegetated than others and required more samples to collect a similar number of vegetation-containing quadrats. In most cases, enough samples were taken on each area to give 20 or more quadrats containing at least one plant.

The harvested plants were taken to the laboratory where measurements were taken on each one to estimate seed production. For *Lepidium*, which has large, distinct fruits with two seeds per fruit, the numbers of fruits per plant were counted. For *Bassia*, *Descurainia* and *Halogeton*, the lengths of inflorescenses (or fruits in the case of *Descurainia*) were measured to the nearest millimeter and recorded for all branches of each plant.

To relate these measurements to seed production, similar lengths of inflorescence were measured and all the seeds removed from the flowering stem and counted. A number of stalks were so measured for each species and the data used to generate a regression of inflorescence length to number of seeds. This was used to estimate seed production per plant, and overall for each plot, based on the inflorescence measurement.

RESULTS

Bassia-Halogeton Comparative Studies

The objective of studies in this section was to elucidate reasons for the occurrence of adjacent pure stands of *Bassia* and *Halogeton* in several areas of the annual communities on the validation site. The majority of the field studies under this topic were conducted on the hill site, with the fence site also being important. Since the sagebrush and bare sites didn't exhibit the abrupt ecotone between pure stands, their role in this portion of the investigation was comparatively minor.

Density at Fixed Points

In order to affirm the observation that there were adjacent, substantially pure stands of *Bassia* and *Halogeton* on the fence and hill sites, plants in dm^2 plots were counted at each of the permanent stakes (spaced in a 5 x 5 m grid) on June 25, 1974. Table 1 displays results of these counts as well as repeat counts taken on May 25, 1975; each total represents five or six quadrats for the hill or fence sites, respectively. The totals, except for the fence plot in 1975, indicate abrupt discontinuities in distribution of *Bassia* and *Halogeton* plants and generally a strong negative association between the two species.

Results of similar density counts taken on the sage and bare sites are presented in Table 2. The area of the sage site is indicated by brackets around the two appropriate rows. The sagebrush undoubtedly influences growth of annual plants, enhancing soil surface physical properties with litter deposition, but also making competition for soil water more keen. On the first sample date in both years, mean densities of plants in the sagebrush vegetation were lower than in the surrounding open areas (1974, 1.8 vs. 7.2 per dm^2; 1975, 6.8 vs. 9.8 per dm^2) although a two-cell chi-square test did not show a significant difference. By the end of the growing season, differences in density had diminished between sagebrush and open areas.

Seeds in Soil

The transect soil seed samples taken across the ecotone on the hill and fence sites in 1974 served not only to estimate the numbers of seed in the soil but also to verify whether or not the abrupt discontinuity in plant distributions extended to distributions of seeds in soil. An accumulation of one species of seed disproportionate to its appearance in the vegetation would indicate a disability of that species to germinate at that point. The data presented in Figure 1 indicate, for the summer of 1974, that seed distributions tend to reflect the vegetation distribution, in that the percentage of *Bassia* seeds in a sample is very much higher in the *Bassia* vegetation; it drops abruptly across the ecotone and is quite low in the *Halogeton* vegetation. The samples contained few seeds other than *Bassia* or *Halogeton*, so percent *Bassia* plus percent *Halogeton* equals 100 in nearly all cases.

Seed Dispersal

Another possible explanation for the persistence of adjacent pure stands of vegetation on the hill site (Table 1) could be lack of seed dispersal by the absent species. *Halogeton* and *Bassia* seeds are quite small (1-2 mm) and light, most likely relying on wind dispersal. An attached, five-winged bract enhances dispersibility of *Halogeton* black seeds, but the brown seeds are enclosed by an appressed bract, making the seed less susceptible to wind movement. *Bassia* fruits have five short hooks which radiate from the central portion of the fruit, allowing them to be carried long distances in fur of animals or on the trouser legs of scientific investigators.

Table 1. Totals of numbers of *Bassia* and *Halogeton* plants established in rows of 1-dm^2 quadrats, and average number of plants per quadrat, on June 15, 1974, and May 25, 1975. Totals represent five or six quadrats for hill or fence sites, respectively. Rows, and quadrats within a row, were both spaced 5 m distant

	Hill Site				Fence Site			
	June 25, 1974		May 25, 1975		June 25, 1974		May 25, 1975	
	Bassia	Halogeton	Bassia	Halogeton	Bassia	Halogeton	Bassia	Halogeton
West row	63	63	6	4	9	126	0	0
	8	54	0	164	31	208	0	0
	6	77	3	199	56	85	0	0
	0	55	0	182	298	1	12	0
	11	123	0	57	198	14	9	0
	75	0	286	0				
East row	88	0	245	0				
Average number per quadrat ± one standard deviation	7.2 ±12.3	10.6 ±14.6	15.4 ±45.9	17.3 ±32.4	19.7 ±24.6	14.5 ±21.8	.7 ±2.35	0 0

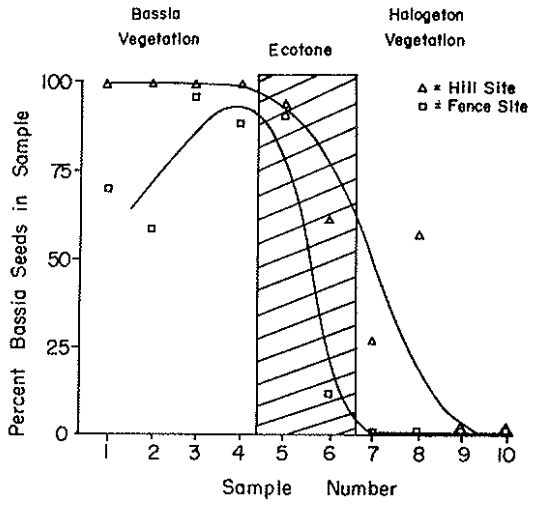


Figure 1. Percent *Bassia* seeds found in ½ of a 300-cc soil sample, to a 3-cm depth, along transects on the hill and fence sites in July. Samples were spaced 1 m apart and two transects were run on each site. Thus, each point represents the mean of two samples. Percent *Halogeton* seeds equals 100 minus percent *Bassia* seeds.

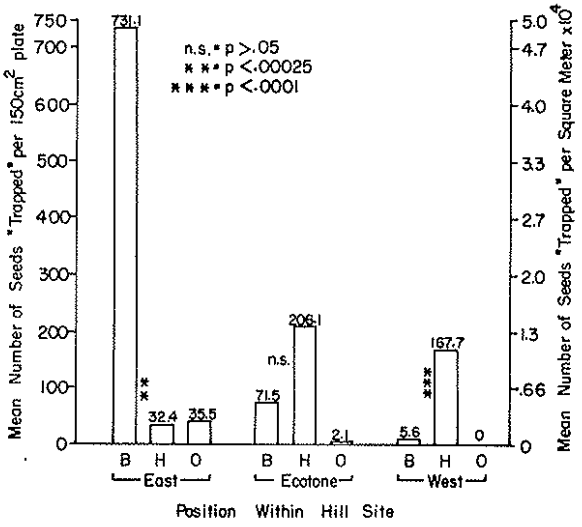


Figure 2. Mean numbers of seeds "trapped" on three rows of 10 x 15 cm metal plates placed on the ground during fall 1974. Each row contained 20 plates; east and west rows were parallel to, and 3 m distant from, the row along the ecotone between *Bassia* and *Halogeton* vegetation. B = *Bassia*, H = *Halogeton*, O = other seed species.

Table 2. Totals of numbers of *Bassia*, *Halogeton* and *Lepidium perfoliatum* plants established in rows of 1-dm² quadrats and average number of plants per quadrat on June 25, 1974, and May 25, 1975. Totals represent five or six quadrats for sage or bare sites, respectively. Rows and quadrats within a row were spaced 5 m distant

	Sage Site				Bare Site			
	June 25, 1974		May 25, 1975		June 25, 1974		May 25, 1975	
	Bassia	Halogeton	Bassia	Halogeton	Bassia	Halogeton	Bassia	Halogeton
West row	4	18	0	18	4	84	2	62
	0	21	0	21	44	24	15	4
	0	20	0	148 L 5[a]	10	0	62	60
	7	2	0	0 L15	38	51	70	11
	0	9	0	48 L 5	52	20	3	107
East row	9	72	0	9				
Average number per quadrat ± one standard deviation	.7 ±2.0	4.7 ±6.8	0	8.1 ±19.8	4.9 ±9.1	6.0 ±8.9	5.1 ±9.3	8.1 ±20.2

[a] L indicates *Lepidium perfoliatum*.

Table 3. Proportion of *Bassia, Halogeton* and other seeds "trapped" on 10 x 15 cm metal plates on the hill site, along the ecotone between *Bassia* and *Halogeton* vegetation and 3 m on either side of this ecotone. There were 20 plates in each row

Proportion of Seeds	East Row	Ecotone	West Row
Bassia	.915	.255	.033
Halogeton	.041	.737	.967
Other species	.044	.008	0
	t=4.05	t=1.78 n.s.	t=5.96

Table 4. Analysis of variance for seed germination percentages of *Bassia* and *Halogeton* in relation to water potential of solutions of sodium chloride or polyethylene glycol through time; at 63 and 97 hr after immersion in the various solutions. n = 5 for all treatment combinations

Source of variation	Degrees of freedom	Mean squares	F value
Time (T)	1	2873.03	26.69**
Species (S)	1	265.23	2.47$^{n.s.}$
Chemical (C)	1	3010.23	27.96**
Osmotic Pressure (OP)	3	46739.09	434.18**
T x S	1	30.63	.28$^{n.s.}$
T x C	1	7.23	.07$^{n.s.}$
T x OP	3	1324.49	12.30**
S x C	1	235.23	2.19$^{n.s.}$
S x OP	3	1693.36	15.73**
C x OP	3	1688.49	15.69**
S x C x OP	3	1122.83	10.43**
T x C x OP	3	126.69	1.18$^{n.s.}$
T x S x C	1	50.63	.47$^{n.s.}$
T x S x OP	3	339.96	3.16*
S x C x T x OP	3	178.09	1.65$^{n.s.}$
Error	128	107.65	
Total	159	1131.39	

n.s. = not significant (P>.05).
* = significant at the 97.5% confidence level.
** = significant at the 99.9% confidence level.

Figure 2 and Table 3 summarize results from the experiment done on the hill site through the fall of 1974, using metal plates coated with a sticky substance which "trapped" seeds contacting it. A two-tailed t-test on each of the data sets from the three sampling positions within the hill site showed the numbers of *Bassia* and *Halogeton* seeds caught to be not significantly different ($P \geq .05$) along the ecotone. However, at positions 3 m east and west of the ecotone row, differences were highly significant ($P < .00025$ and $P < .0001$, respectively). This seems striking, considering the ecotone ranged in width from about 1.5-2.5 m and plants of the less abundant species were frequently within 2 m of either the east or west row of plates. However, the literature contains many examples of extremely limited seed dispersal from parent plants (Friedman and Orshan 1975; Werner 1975).

The seemingly short dispersal distances can be attributed partly to the presence of a polygonal soil surface structure with cracks up to several centimeters deep separating the peds. Seeds blown along the surface will usually fall into a crack after moving only 20-30 cm, preventing further movement. A high percentage of plants which successfully establish in spring are found emerging from these cracks. The explanation for this seedling distribution may simply be that most of the seeds end up in the cracks; or the cracks may provide a more favorable germination-establishment microenvironment.

Seed Germination

One possible reason for persistence of the adjacent pure stands of vegetation, allowing for some dispersal into the bordering stand, might be differences in germinability of the two seed species. Heterogeneity in soil surface microenvironmental conditions might favor germination of one species or the other from point to point within the annuals community. One species could be screened out of an area by an inability to germinate there. Both laboratory and field investigations were done to study germination behavior under different conditions.

Simulated moisture areas—Preliminary tests in petri dishes showed that *Bassia* seeds germinated freely (90-95%) in tap water, as did *Halogeton* black seeds after a six-week, cold-moist treatment (Cronin 1973). This experiment investigated germinability through time at different levels of water potential and in sodium chloride (ionic) and polyethylene glycol (chemically inert) solutions. Figures 3 and 4 and Table 4 summarize results and present statistical analysis for this experiment. From the graphs it is evident that germination takes longer in the low water potential solutions (—15, —20 bars); that sodium chloride permits a higher germination percentage than polyethylene glycol; and that the general trend in germinability for both species is about the same.

The factorial analysis of variance (Table 4) bears out the latter point, indicating no significant difference in germinability of the two species. Differences in all of the other main effects were highly significant, however, as were several of the interaction terms. Significant differences due to time (63 vs. 97 hr) and osmotic pressure (—5 to — 20 bars) were to be expected, given the slower imbibition rate at lower water potential, but the difference due to the two chemicals is more interesting.

Several authors (Parmar and Moore 1966; Wood et al. 1976; Young et al. 1968) have germinated seeds in polyethylene glycol and/or sodium chloride solutions. Due to its chemical inertness, polyethylene glycol usually gives higher germination percentages than does the sometimes

toxic sodium chloride. Contrastingly, these halophytic species germinated significantly better in salt solutions. This salt enhancement of germination may have some physiological basis in seed germination processes.

Several significant interaction terms support and clarify the main effect differences. There are differences in species response to osmotic pressure, time and chemical effects, as three of the interaction terms incorporating species were significant. Several other interactions involving species were not significant. The other notable significant interaction is chemical x oxmotic pressure, indicating that germination response was not the same in the two chemical solutions at different levels of osmotic pressure.

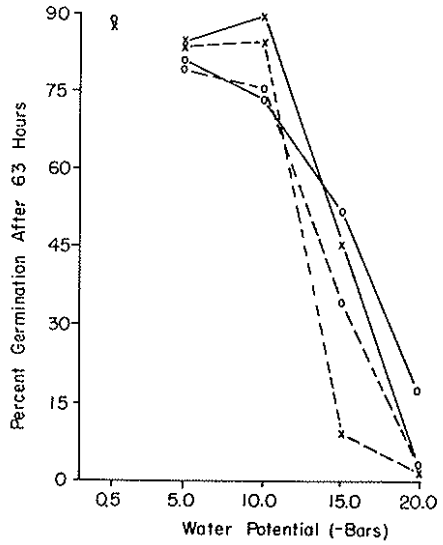


Figure 3. Percent germination after 63 hr of *Bassia* (O) and *Halogeton* (X) seeds in sodium chloride (———, ionic) and polyethylene glycol (— — —, nonionic) solutions of different water potential. n = 5 for each treatment with 50 seeds per dish.

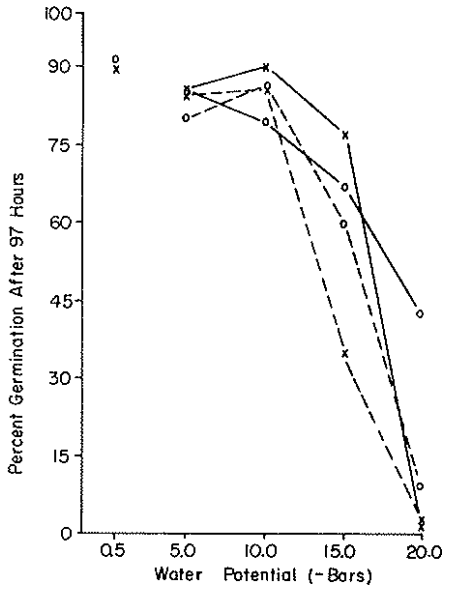


Figure 4. Percent germination after 97 hr of *Bassia* (O) and *Halogeton* (X) seeds in sodium chloride (———, ionic) and polyethylene glycol (— — —, nonionic) solutions of different water potential. n = 5 for each treatment with 50 seeds per dish.

Field studies—Corroboration of the above laboratory experiment on seed germination is provided by results of a field experiment in which Saran mesh packets were buried at 1- and 3-cm depths. The data in Table 5 evidence a very low and fairly uniform percent recovery of hard seeds. Mesh size of the packets was too small for seeds to fall out. Considerable care was taken to locate all hard seeds with each seed packet. During this process of microscopic examination, numerous seed coats were found, indicating germination had taken place; thus, it can be inferred that the few remaining hard seeds were the only seeds which had failed to germinate.

The only "trend" in the data, if it can be called that, is that a few more *Bassia* seeds were recovered from the *Halogeton* vegetation type. The differences between *Bassia* and *Halogeton* are not statistically significant.

Taken together, these experiments on seed germination under laboratory and field conditions provide substantial evidence that there are no important differences in germinability of the two species under the test conditions. Persistence of adjacent pure stands of *Bassia* and *Halogeton* cannot be attributed to an inability of one species to germinate in the other vegetation type.

Seedling Establishment Success

Natural populations of plants growing from seed are most likely to suffer mortality during the establishment phase of the life cycle (Harper 1967). At this stage, the plant must begin photosynthesis as seed energy reserves are nearly exhausted; its root has not yet penetrated deeply enough to ensure a reliable water supply; and anatomically it has not hardened sufficiently to be extremely resistant to physical stresses. The microenvironment about the seedling is extremely important in determining whether establishment will occur.

With the above ideas in mind, results of the experiment on seedling establishment are quite informative. On December 20, 1974, seeds were sown onto the soil surface of marked quadrats which had been covered during the fall seed dispersal period. On May 16, 1975, these quadrats were censused to see how many plants had become established in them.

Figure 5 summarizes these data for the four study sites and Table 6 present χ^2 values for statistical tests that were done on the data. Germination studies in the laboratory and field, as just related, indicated a uniformly high germinability (92-97%) for both species under test conditions. Assuming this occurred, the null hypothesis tested here was that establishment success was equal for both species. Only in the *Halogeton* vegetation type of the fence site was there no significant difference between total

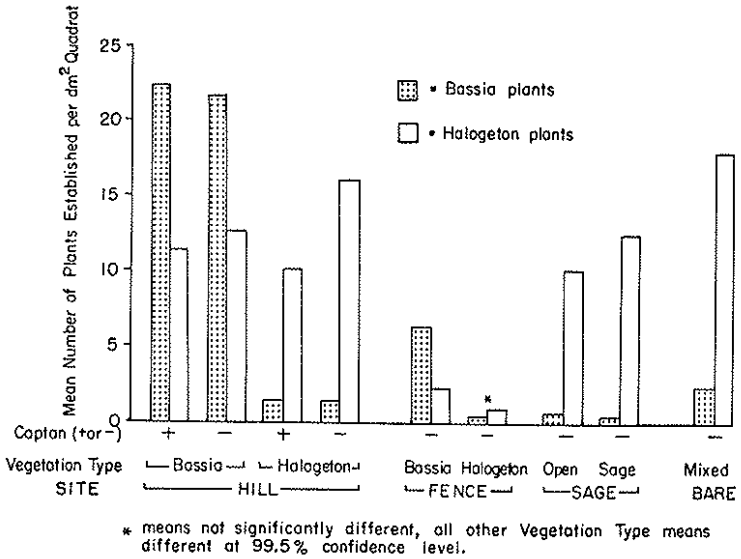


Figure 5. Mean numbers of *Bassia* and *Halogeton* plants established in the field on May 16, 1975, in different vegetation types on the study sites. One-hundred seeds of each species were sown into each dm^2 quadrat. n = 10 for all vegetation types except the bare site in which n = 15.

numbers of *Bassia* and *Halogeton* plants established. This site also had the lowest establishment percentage, indicating it was most "severe." In all other study areas, either *Bassia* or *Halogeton* established significantly better than the other species. In general, establishment success of *Halogeton* was better than that of *Bassia*; only on two areas (*Bassia* vegetation on hill and fence sites) did *Bassia* establish significantly better than *Halogeton*.

On the hill site, each vegetation type received an additional group of seeds which had been treated with the fungicide Captan. Greater establishment of Captan-treated seeds would have been an indication that fungal decay decreased numbers of viable, untreated seeds. This was not the case though, and after performing a χ^2 test for independence on Captan-treated vs. non-Captan-treated seeds, which indicated homogeneous data, the data were combined for other statistical tests.

Three more χ^2 tests, for independence or interaction, were done using all the data from the hill, fence and sagebrush sites to test if establishment behavior of the two species was the same in both vegetation types of each site. For both hill and fence sites the test was significant, indicating that the species established with different degrees of success in the two vegetation types. For the sagebrush site, the test showed no interaction; that is, both species established to the same extent near the sagebrush canopies and in open areas away from sagebrush.

The same χ^2 tests using data from August 31, 1975, of repeated observations of these plots, generally had lower χ^2 values (Table 6). This indicates that differences within the quadrats, in terms of numbers of plants growing there, had diminished through the summer. In nearly all cases these lessened differences were due to a greater mortality of the more abundantly established species in the various vegetation types (Table 7). This is not unexpected as an individual of the dominant species will experience a greater degree of intraspecific competition, having more neighbors of the same species which require essentially the same resources. Contrastingly, the subordinate species survive better, presumably due to less competitive stress, assuming its resource requirements are somewhat different from the dominant species.

Table 5. Mean number of hard seeds recovered from Saran mesh packets buried in the soil at 1- and 3-cm depths in December 1974 and recovered in May 1975. n = 3 for each treatment combination; each packet contained 100 seeds when buried so number recovered = percent recovered

	Vegetation Type			
	Bassia		Halogeton	
Depth	Seed species		Seed species	
	Bassia	Halogeton	Bassia	Halogeton
1 centimeter	2.3±2.1	2.7±2.1	4.3±3.5	.7±1.2
3 centimeters	2.7±1.5	3.0±1.0	7.7±9.9	0

Most interesting, though, are the relative amounts of establishment and survival success by the two species shown in Table 7. Overall percent mortality for the two species is similar, 52% for *Bassia* versus 56% for *Halogeton*, but the absolute numbers involved are quite different. Only 576 *Bassia* plants became established but 1019 *Halogeton* plants did; a two-cell χ^2 test shows these numbers to be significantly different at the 99.9% confidence level. The year-end values of 274 *Bassia* versus 446 *Halogeton* surviving are also significantly different at the 99.9% confidence level. Thus,

although equal numbers of seeds of both species were sown into various sites in the field, about 1.8 times more *Halogeton* plants established and survived to maturity than did *Bassia* plants.

Again referring to Figure 5, the mean number of plants established per dm^2 quadrat is also equal to percent establishment as there were 100 seeds of each species in each quadrat. The low establishment, averaging 8% over all quadrats and ranging from 0.4 to 22%, indicates that a very large portion of seeds in soil never become established as plants. Many of these seedlings emerge from soil only to die within a short time thereafter. On May 16, when first counts of plant establishment were made, nearly all of the quadrats contained evidence of from two to five times as many dead seedlings as live plants. Cronin (1965) previously documented this high establishment mortality for *Halogeton*.

Drought Tolerance

During the establishment phase, and throughout the growth cycle, the ability to tolerate drought is particularly important for survival of plants in arid areas. Distributions of many species are limited by insufficient amounts of water at some critical phase of the growth cycle. *Halogeton's* succulent habit was a clue to a possible ability to withstand moisture stress.

In Table 8, results of the comparative study on drought tolerance between *Bassia* and *Halogeton* are summarized. The data verify *Halogeton's* presumed drought tolerance, in that its survival percentage was always greater for treatments in which it withstood more days of drought and in which the minimum soil water percent content was lower than for the comparable *Bassia* treatment.

The data on plant dry weights are more difficult to interpret and are confounded by density effects, as after the water stress period, pots had different numbers of survivors. All plants grew about the same length of time from seed (six to seven weeks) and each of the drought treatments received water at the "control" rate for two weeks after the end of its drought. Since dry weights of *Bassia* and *Halogeton* control plants were not greatly different, one might assume that dry weights of comparably droughted plants should also be similar. This was not the case, as dry weights of droughted *Halogeton* plants were significantly less than those for *Bassia*.

These differences may simply have been due to the fact that the pots containing *Halogeton* were more crowded, since fewer had died during the drought period, and therefore each plant grew less. Another explanation might be that the *Bassia* plants, despite their susceptibility to mortality, were more resilient and resumed normal growth rates more rapidly than did *Halogeton*, enabling them to accumulate greater biomass. A third explanation could be that the longer and drier drought treatments *Halogeton* withstood caused its rate of recovery to be slower, perhaps due to greater physiological dysfunction. A combination of the above hypotheses may explain most of *Halogeton's* relatively poor recovery from drought.

Soils Analyses

Several types of analyses were performed on soils, mainly from the hill site, to compare parameters in the *Bassia* and *Halogeton* vegetation types which might correlate with the above differences in seedling establishment success and drought tolerance. An additional aspect was an investigation of the role of cracks between soil surface polygonal peds in relation to seedling germination and seed burial.

Profile descriptions and analytical data—Appendix II contains descriptions of soil profiles in the *Bassia* and *Halogeton* vegetation types on the hill site. The two profiles are generally similar and display little development of distinct horizons. Noticeable dissimilarities are most pronounced at the soil surface where seedling establishment takes place. The *Bassia* surface is covered with a thin litter layer which is largely absent under *Halogeton* vegetation.

The surface horizon under *Halogeton* contained numerous gas-filled vesicles to a depth of 3-6 cm which were not present under *Bassia* vegetation. Blackburn and Skau (1974) discuss several characteristics of surficial vesicular horizons which adversely affect plant establishment and which will be considered later. A moderate fine platy structure accompanied the vesicular horizon and is likely more of an impediment to root penetration than the subangular blocky-fine granular structure present under *Bassia*. These comments also apply to the soil surface on the fence site, as observations there showed definite similarities to the hill site.

The whole profile for *Bassia* soil is generally darker than the *Halogeton* profile, perhaps due to a higher percentage of organic carbon under *Bassia* and high exchangeable sodium percentage under *Halogeton*. Both profiles are calcareous throughout, the abundance of calcium increasing with depth.

Analytical data—Samples of soil were collected from three depths for two different profiles in the two vegetation types of the hill site for analysis regarding several pertinent parameters. Table 9 presents results of these analyses, wherein the mean is listed for the two profiles in each vegetation type; values from the two profiles were very close so the means have very low variances.

There are several striking differences in these data considering the profiles are no more than 10 to 12 m distant. The high exchangeable sodium percentage, bulk density and low percent organic carbon for the *Halogeton* surface soil collectively provide evidence for an unfavorable seedling establishment microenvironment. Soils with more than 15% exchangeable sodium are classified as sodic (Hausenbuiller 1972) and create considerable problems for growth of most plants. The principal effect here is unfavorable surface physical properties created by dispersion of clay and deflocculation of soil colloidal particles. This creates a dense, impenetrable surface crust which is less permeable to air and water and greatly hinders emergence of seedlings.

Table 6. χ^2 values testing establishment and summer survival success for sown *Bassia* and *Halogeton* seeds in dm² quadrats in different vegetation types at the beginning and end of the growing season in 1975. n = 10 for sage and fence sites, 15 for bare site and 20 for hill site. d.f. = 1 in all cases

Site	Vegetation Type	May 16 χ^2 (d.f.=1)	May 16 Interaction χ^2 (d.f.=1)	August 31 χ^2 (d.f.=1)	August 31 Interaction χ^2 (d.f.=1)
HILL (Captan data pooled)			246.0**		211.8**
	Bassia	58.1**		115.0**	
	Halogeton	188.9**		97.7**	
FENCE			6.4*		9.2**
	Bassia	18.8**		14.2**	
	Halogeton	1.1 n.s.		2.3 n.s.	
SAGE			.4 n.s.		.7 n.s.
	Open (Halogeton)	81.6**		34.0**	
	Sage	110.6**		35.0**	
BARE					
	Mixed	175.6**		82.1**	

n.s. = not significant.
** = significant at 99.5% confidence level.
* = significant at 97.5% confidence level.

Table 7. Total plants established in dm² quadrats on May 16, 1975, from seed sown in December 1975; numbers of plants surviving to August 30, 1975; numbers dying and percentage dying through the summer. Each quadrat was sown with 100 seeds of each species. n = 10 for all vegetation sites except for the bare site, in which n = 15 quadrats

Site	Vegetation Type	Total Plants Present May 16 Bassia	May 16 Halogeton	August 31 Bassia	August 31 Halogeton	Number Dying Through Summer Bassia	Number Dying Through Summer Halogeton	Percent Dying Through Summer Bassia	Percent Dying Through Summer Halogeton
HILL	Bassia	215	125	97	20	118	105	55	84
	Bassia (captan)	222	113	91	9	131	104	59	92
	Halogeton	12	159	12	104	0	55	0	35
	Halogeton (captan)	14	100	10	48	4	52	29	52
FENCE	Bassia	63	22	35	9	28	13	44	59
	Halogeton	4	8	1	6	3	2	75	25
SAGE	Open (Halogeton)	6	100	6	51	0	49	0	49
	Sage	4	124	2	66	2	58	50	47
BARE	Mixed	36	268	20	133	16	135	44	50
Totals		576*	1019*	274*	446*	302	573		
						Overall Percent Dying:		52	56

*Significant at 99.9% confidence level.

Table 8. Duration of drought treatments, minimum water contents (gravimetric), survival percentages and mean plant dry weights at harvest (2 weeks after termination of drought and 6-7 weeks after seed sowing) for *Bassia* and *Halogeton* grown in pots in the greenhouse during September and October 1975. n = 4 for all treatments and each pot initially contained 25 plants. Means followed by the same letter are not significantly different at the 95% confidence level, using Duncan's multiple range test

Species	Duration of Drought (days)	Mean Minimum soil water percent content	Mean survival percent	Mean dry weight per plant at harvest (mg)
Bassia	None	15	100	143[a]
	10	2.9±.2	81±11.9	116[a]
	12	2.5±.2	72±22.4	128[a]
	14	1.9±.3	0	
Halogeton	None	15	100	125[a]
	16	2.6±.1	97±3.8	56[b]
	18	2.1±.2	95±3.8	61[b]
	20	1.7±.1	87±13.0	41[b]

Table 9. Results of tests on various soil physical and chemical parameters. Each datum is the mean value from two different profiles in each vegetation type, except for bulk density, in which four samples were taken

Soil type and depth	Bulk density	Percent organic carbon	Exchangeable sodium percent	mmhos/cm EC_e	Base saturation percent	CEC	pH
Bassia Soil							
0-3 cm	.89±13* (0-5 cm)	3.4	1	1.1	60	16.4	7.7
14-15 cm		1.7	2	.6	53	17.5	7.8
29-30 cm		1.4	2	.6	64	14.3	7.7
Halogeton Soil							
0-3 cm	1.16±.11* (0-5 cm)	1.5	16.5	1.7	44	10.9	8.5
14-15 cm		.8	13.5	.9	38	10.9	8.7
29-30 cm		.7	55	14.3	41	11.3	7.8

* Means significantly different at the 99 percent confidence level. n = 4.

Although bulk density was significantly greater at the *Halogeton* soil surface, the measurement probably does not reflect the difference present at the microsite level, since bulk density was averaged over the upper 5 cm of soil. It is generally accepted that *Halogeton* acts as a "sodium pump" by accumulating high concentrations of sodium in its tissues which are leached to the surface soil upon decomposition of litter (Kinsinger and Eckert 1961); thus, an exchangeable sodium percentage and concomitant bulk density for the topmost centimeter or half-centimeter of *Halogeton* soil might produce considerably greater values than those shown in Table 9. These data would more closely represent the microenvironment at a scale relevant to seedling emergence and establishment, and would contrast even more sharply with the data from the *Bassia* soil. By comparison, the *Bassia* soil surface parameters of exchangeable sodium percentage, bulk density and percent organic carbon characterize a favorable site for seedling establishment.

Dissimilarities are evident in the other parameters but their magnitude makes them unimportant, regarding seedling establishment, relative to the parameters just discussed.

To the 30-cm depth, it is evident that the soil profiles have a different chemistry throughout. All measured parameters indicate the *Bassia* profile should be more favorable to plant growth, with its lower pH and electrical conductivity and higher cation exchange capacity and base saturation percentage. By comparison, the *Halogeton* profile is sodic throughout with the ionic salts becoming a definite problem at the 30-cm depth. Nutrient availability here will be lower due to the lower organic carbon percentage, base saturation percentage and cation exchange capacity.

Field water potential—To see if the previously described differences in drought tolerance of the species might relate to their distribution in the field, a series of measurements of soil water potential was taken in the pure vegetation types of the hill site. Psychrometers buried at a 12-cm depth showed sharply contrasting patterns of soil water potential during the summer of 1975. Figure 6 summarizes the field data and plainly shows the much drier condition of the *Halogeton* soil from the end of June onward. During the middle part of June (20-26), water potential under *Halogeton* is rapidly decreasing, but is not as low as in the *Bassia* vegetation.

These data were separated into two groups, with June 26 being the dividing point, and statistically tested using analysis of covariance techniques, with Julian date being the covariate. This improved the resolution of the analysis by removing variation common to both sites due to the summer-long trend of soil water depletion. The analyses showed, at the 99.9% confidence level, that the *Halogeton* soil was significantly wetter than the *Bassia* soil prior to June 26, but significantly drier after this date.

Recalling the results of the drought tolerance experiment, it would seem that the less drought-resistant *Bassia* would have a more difficult time growing in the drier *Halogeton* soil. Seed production also might be diminished here since seed is not produced until the end of summer, the driest part of the year.

A fairly reasonable explanation can be advanced for the wetter *Halogeton* soil in mid-June. There are two factors of importance here: the first is the higher position (30-60 cm) of the *Halogeton* site; the second is the presence on the *Bassia* site of a luxuriant stand of the early maturing *Descurainia*. Relatively abundant soil water early in the growing season would allow capillary movement to the elevated *Halogeton* site, maintaining it relatively wetter. In addition, the rapidly growing *Descurainia* were likely transpiring significant amounts of water from the *Bassia* site in order to complete their life cycle in early July.

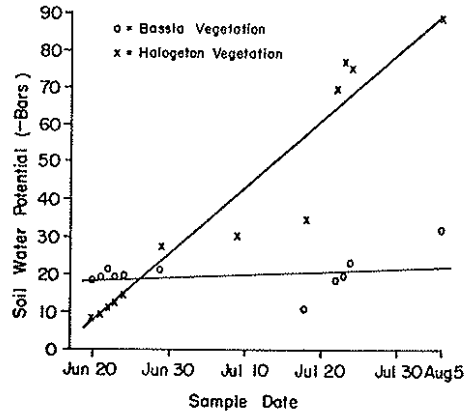


Figure 6. Seasonal trend of soil water potential at 12-cm depth on the hill site in *Bassia* (O) and *Halogeton* (X) vegetation. n for each sample point varies from 2 to 4.

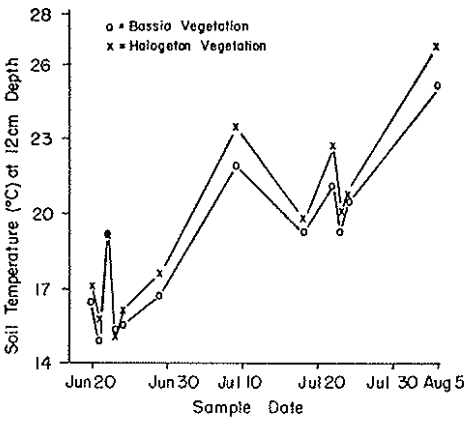


Figure 7. Seasonal trend of soil temperature at 12-cm depth on the hill site in *Bassia* (O) and *Halogeton* (X) vegetation. n for each sample point varies from 2 to 4. Covariance analysis shows the *Halogeton* soil to be significantly warmer at the 97.5% confidence level, F = 6.307.

Soil temperature—Concomitant with the water potential differences in the two sites were soil temperature differences as shown in Figure 7. The graph shows readings taken around midday, for the sake of clarity. But it was evident that *Bassia* soils were almost always 1 to 2 C cooler than the *Halogeton* soils, regardless of the time of day the readings were taken. An analysis of covariance similar to the one just described, with Julian dates as the covariate, showed soil temperatures to be significantly different at the 97.5% confidence level. The overall adjusted means were 20.2 and 19.0 C for the *Halogeton* and *Bassia* soils, respectively. This slight, but significant, difference is another indication of the more advantageous *Bassia* soil environment in relation to plant growth.

Comparison of crack and ped germination sites—There was a distinctive pattern of seedling establishment, the preponderance of plants emerging from the cracks between soil peds; this investigation attempted to measure differences in soil temperature and water potential between the crack and ped germination sites. The hypothesis was that cracks served as concentration zones for water from snowmelt and, as such, would provide cooler, wetter germination sites than a position at the same depth but under a soil ped. As stated earlier, bihourly sampling commenced at the end of a two-day rainy period followed by a warming trend.

An analysis of variance using a block design to remove parallel variation in readings due to daily and hourly variation in water potential at the measurement sites was not conclusive. Table 10 shows that through the sampling period, some of the psychrometer pairs showed no significant difference in water potential at the crack and ped microsites, while other pairs showed cracks to be significantly wetter or vice versa. Overall, within each vegetation type, crack and ped microsite means were not significantly different. However, there was a significant difference ($P < .001$) overall in water potential between the two vegetation types, the *Halogeton* sites being wetter than the *Bassia* sites. This supports the 12-cm-depth water potential measurements discussed above, for mid-June. There were no detectable patterns of difference in soil temperatures.

The outcome of this investigation does not allow generalization about soil temperature or water potential at crack or ped microsite locations due to heterogeneity in the readings obtained. Considerably more sophisticated sampling instruments and techniques might be able to demonstrate more pronounced differences between crack and ped germination sites, but the magnitude of differences might not be biologically meaningful. Point-to-point variation in physical parameters at the soil surface is great and undoubtedly affects establishment success of plant species.

Photo comparisons of polygonal ped structures—It was not possible to make extremely quantitative comparisons of positions of cracks between soil surface ped structures due to shadows on some of the photographs and a slight difference in scale for the two different years. It was evident that there was little change in the positions of cracks or the shapes of peds from 1974 to 1975. This is to be expected when it is realized that the cracks represent lines of weakness between the more cohesive polygonal surface peds. Once cleaving occurred along a given line, despite swelling of clays in fall and winter, it might be expected that the original cleavage line would be maintained and reinforced along the original lines of weakness between peds.

Hugie and Passey (1964) indicate that on their study sites in the northern Utah-southern Idaho region, the cracks between surface peds became less distinct through fall and winter but did not close completely. Their observations and the photographic comparisons seem to indicate that cracks are fairly permanent structures, at least from one year to the next. As such, they wouldn't cause many seeds to become buried so deeply in the soil (3-6 cm) that successful emergence would be prevented the following spring.

Table 10. Mean water potentials in crack and ped sites for four pairs of psychrometers in *Bassia* and *Halogeton* vegetation on the hill site. Readings were taken at bihourly intervals from June 20 through 24, 1975

	Crack		Ped
Bassia Sites			
1	18.3	n.s.	17.4
2	31.8	**	25.9
3	26.3	n.s.	27.9
4	27.5	n.s.	29.0
Average	26.0	n.s.	25.1
Halogeton Sites			
1	8.8	*	7.3
2	5.6	*	3.9
3	28.9	n.s.	23.4
4	32.8	n.s.	31.0
Average	19.0	n.s.	16.4

* = significantly different at the 95% confidence level.
** = significantly different at the 99.9% confidence level.
n.s. = not significantly different.

Competition Experiments

Field watering of plants—The ability of plants to respond to supplemental moisture can be an index of their competitive ability, particularly if one species responds with greater growth increases than another. Results of this experiment, conducted along the *Bassia-Halogeton* ecotone of the fence site, are informative regarding field growth behavior in a dry year (1974).

Figures 8, 9 and 10 present results of this watering experiment with information on plant density, per plant dry weight, and dry weight per square decimeter, respectively. All three figures reveal the striking response of *Halogeton* to added water. *Bassia*'s response to water is almost undetectable, with only slight differences in its density and biomass in watered and unwatered plots.

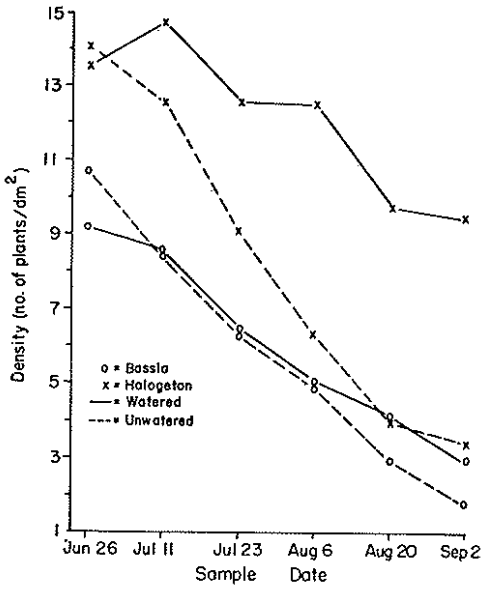


Figure 8. Densities of *Bassia* (O) and *Halogeton* (X) plants under water supplements (———; 25 mm equivalent per week) or nonwater supplemented (— — —) conditions in the field. Plants grew together and sampled areas were 1 dm². n = 22 in most cases, but drops to 18, 14, 10 and 8 for the watered plots over the last four sample dates.

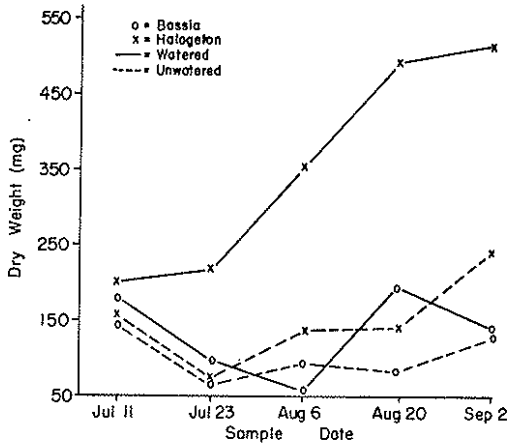


Figure 9. Average dry weights of *Bassia* (O) and *Halogeton* (X) plants under water-supplemented (———) or nonwater supplemented (— — —) conditions in the field. Plants grew together in the field plots. n = 30 in all cases.

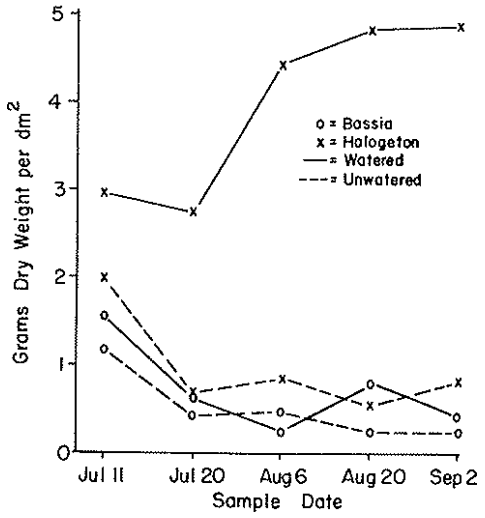


Figure 10. Grams dry weight plant material per dm² for *Bassia* (O) and *Halogeton* (X) under water-supplemented (———; 25 mm equivalent per week) or nonwater-supplemented (— — —) conditions in the field. n = 30 for individual plant weights; n = 22 to 8 for density.

Starting from comparable initial densities (Fig. 8) on June 26, the watered *Halogeton* plants show a much slower rate of density decline than any of the other treatments. Table 11 shows results of analysis of variance of this density data, all three of the main effects being significant. Time of harvest caused a significant difference in density as did the watering treatment, and the two plant species. The only significant interaction term was the water x species term, which is understandable due to the dissimilar density responses of watered *Bassia* and *Halogeton* plants.

Figure 9 provides more evidence of *Halogeton*'s strong response to water in that individuals were able to accumulate significantly greater dry weight biomass, from essentially similar initial weights. Analysis of variance of these data showed all of the main effects and interaction terms, including the three-way interaction, to be significant. The significant time x water and time x species interactions may be due to the seemingly strange behavior of the watered *Bassia* plants. The *Bassia* pattern of weights (Fig. 9) is likely an artifact due to the destructive sampling procedure. At each sample period, plants were harvested from new plots, and this between-plot variability seemed particularly high for the watered *Bassia* treatment. In contrast, *Halogeton*'s growth response to water is very conspicuous.

Figure 10 was generated from Figures 8 and 9 by multiplying density times per plant dry weight. It shows even more markedly the dominance of the watered *Halogeton* plants on a grams per square decimeter basis, due to slowest rate of density decline and highest per plant biomass. Again, there are no noticeable trends in the other treatments.

Growth chamber studies—Although the experimental design and the methods used in the two growth chamber competition studies were the same, the experimental factors being investigated were different. In the first study, stands of plants were either pure *Bassia* or *Halogeton* or of three intermediate proportions. In mixed pots, seeds were either sown at the same time or one seed species was sown eight days earlier or later than the other, and plants were grown about 119 days from seed to harvest. All plants were grown in soil which had been collected where both species grew commonly.

In the second study, plants were grown on the two different soils from the hill site in pure stands or in a mixed stand with equal numbers of both species. The other experimental factor was three levels of increasing water availability. These plants were grown only 57 days from seed to harvest.

Timing-proportions study—The objectives of this study were to investigate the effect on plant dry weight production of different stand proportions and to see if an eight-day difference in time of growth initiation would influence dry weight while in competition with the other species. These objectives have realistic field implications in that certain areas of vegetation happen to have different ratios of the two species growing proximate to each other; adjacent germination microsites, coupled with dissimilar germination requirements, could easily allow one species to commence growth eight days earlier or later than the other.

Figure 11 summarizes results of this experiment, measured in milligrams dry weight per plant, for *Bassia*, and Figure 12 presents the same information for *Halogeton*. In both figures, the pure stand pots have been graphed across the timing axis, for clarity, although these pots contained only one species and hence had no timing aspect. Points with the same letter are not significantly different at the 95% confidence level by Duncan's multiple range test.

The results show, for *Bassia*, that the proportion of plants in pots was very important in affecting mean plant dry weight; that is, pots contining few *Bassia* plants had much larger plants. Over the 119 days that the plants were grown, the eight-day differential in seed sowing had almost no effect. The most interesting thing, though, is that the pure-stand plants were less productive than any of the mixed-pot treatments. That is to say, for *Bassia*, interspecific competition was less intense than intraspecific competition since individuals were able to accumulate more weight when grown with *Halogeton*.

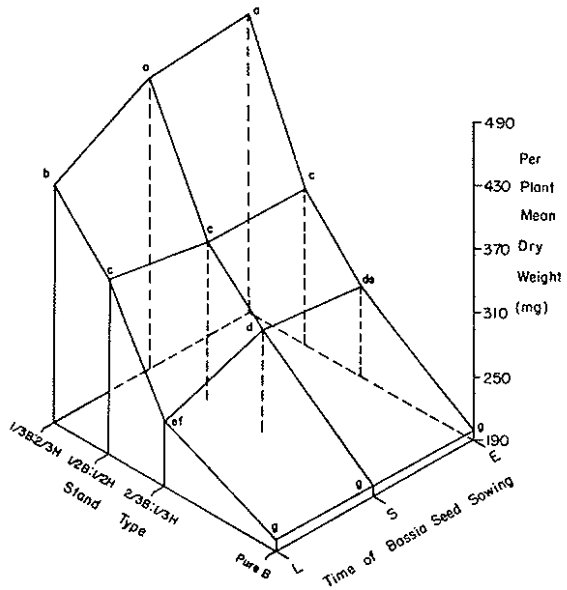


Figure 11. Mean dry weight (mg) of *Bassia* plants grown in field soil in which both *Halogeton* and *Bassia* grew. Each dm^2 pot contained 36 plants but the number of *Bassia* plants varied, being either 36, 24, 18, 12 or 0, with *Halogeton* comprising the remaining fraction. In mixed pots, *Bassia* seeds were sown at the same time or eight days earlier or later than *Halogeton* seeds. The "pure" stand type is graphed across the timing axis, in order to clarify the graph, though there was no timing aspect in the "pure" treatment. n = 4 in all cases. Plants were harvested 119 days after seed sowing, or 112 days in case of late-sown seed.

Table 11. Analysis of variance for plant densities in dm^2 quadrats in the field for *Bassia* and *Halogeton*, through time and with or without supplemental watering

Source of variation	Degrees of freedom	Mean squares	F value
Time (T)	5	605.80	21.87*
Water (W)	1	433.59	15.65*
Species (S)	1	1868.81	67.44*
T x W	5	54.19	1.95 n.s.
T x S	5	5.72	.21 n.s.
W x S	1	318.34	11.49*
T x W x S	5	19.18	.69 n.s.
Error	428	27.70	
Total	451	41.75	

n.s. = not significant.
* = significant at the 99.9% confidence level.

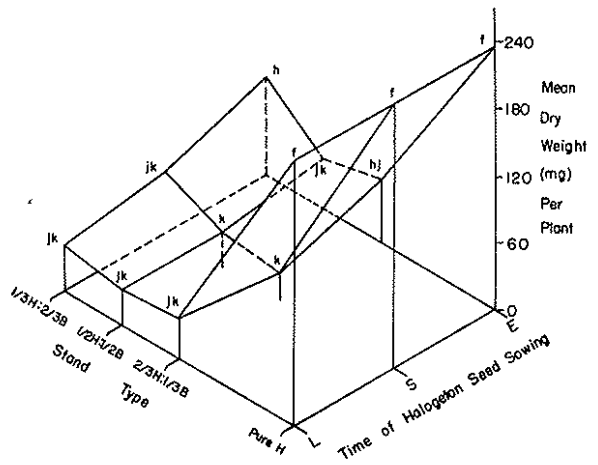


Figure 12. Mean dry weight (mg) of *Halogeton* plants grown in field soil in which both *Bassia* and *Halogeton* grew. Each dm^2 pot contained 36 plants but the number of *Halogeton* plants varied, being either 36, 24, 18, 12 or 0, with *Bassia* comprising the remaining fraction. In mixed pots, *Halogeton* seeds were sown at the same time or eight days earlier or later than *Bassia* seeds. The "pure" stand type is graphed across the timing axis, in order to clarify the graph, though there was no timing aspect in the "pure" treatment. n = 4 in all cases. Plants were harvested 119 days after seed sowing, or 112 days in case of late-sown seed.

The results for *Halogeton* mixed pots in Figure 12 are not surprising after considering *Bassia*'s behavior. *Halogeton* shows only slight response to the differing proportions, implying that, in all cases, it faced stiff competition. This is evident by comparing the milligram scales for the two figures; it immediately becomes apparent that mean *Halogeton* weights ranged from about one-fifth to one-tenth of those for *Bassia*. The data provide a clear indication of the competitive superiority of *Bassia* under growth chamber conditions.

This strong evidence cannot be explained away with supposition that the growth chamber conditions were inherently unfavorable to *Halogeton*. By comparing dry weights of plants in pure stands for the species, it is demonstrated that *Halogeton* was significantly more productive than *Bassia* ($\bar{x}$ = 238 vs. 198 mg per plant). Thus, the competitive superiority of *Bassia* is real and may be due to an advantage in root function. There seemed to be little differential due to competition for light as *Halogeton* plants in the middle of pots, closely surrounded by other plants, grew as well as those at the frequently more open edges of pots. The evidence seems to point to the ability of *Bassia* to usurp soil resources to the detriment of *Halogeton*'s growth.

The statistical analysis of Table 12 supports the evidence shown in the two figures. There were slightly significant differences ($P<<.001$) due to the species and proportions of plants in pots, but no significant difference due to the timing of seed sowing. It seems that over a fairly long growth period (119 days), the eight-day difference in seed sowing was not very important. However, *Halogeton* did respond with marginally noticeable growth differences due to the timing effect, as indicated by the significant species x timing interaction. The significant species x proportion interaction was to be expected and the significant three-way interaction is not surprising, due to the complex response surfaces of the species. Pure-stand pots were not included in this analysis, as they would have made the design unbalanced since there was no timing factor in their treatment. Their analysis was run separately with mixed pots in which seeds were sown at the same time, so that the design would be balanced. These F-tests indicated the same results as Table 12.

Soil-watering levels study—Additional factors investigated in this experiment were the responses of the two species when grown on the two contrasting soils from the hill site and to increasing water availability, when grown in a growth chamber. There was only one proportion of mixed pots here and plants were grown only 57 days.

Early on in the experiment a striking difference became apparent in growth of both species on the two soils. Figures 13 and 14 show pure-stand *Bassia* and *Halogeton* plants from the contrasting soils after about one month's growth. It is very evident that both species have made greater growth on the *Bassia* soil. This is not surprising recalling differences in soil chemistry shown in Table 9.

Table 12. Analysis of variance for mean plant dry weight comparing *Bassia* and *Halogeton* plants grown in mixed stands of three proportions, with seeds of one species sown at the same time or eight days earlier or later than the other species. There were four replicates per treatment combination and 36 plants per pot

Source of variation	Degrees of freedom	Mean squares	F value
Species (S)	1	1.72	5456.06*
Timing (T)	2	4.24×10^{-5}	.13 n.s.
Proportion (P)	2	6.14×10^{-2}	194.87*
S x T	2	4.50×10^{-3}	14.28*
S x P	2	3.67×10^{-2}	116.30*
T x P	4	3.56×10^{-4}	1.13 n.s.
S x T x P	4	1.85×10^{-3}	5.89*
Error		3.15×10^{-4}	
Total		2.75×10^{-2}	

n.s. = not significantly different.
* = significantly different at the 99.9% confidence level.

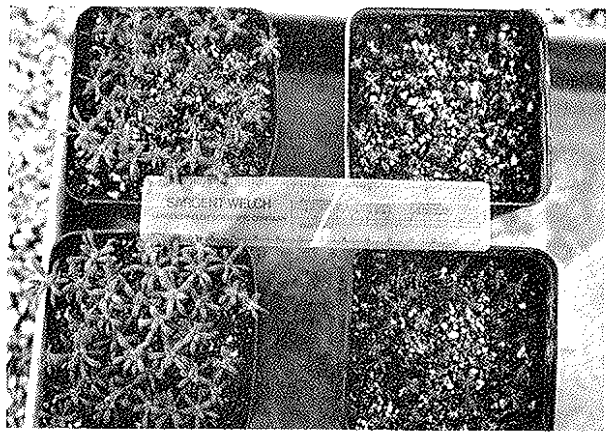


Figure 13. Photograph showing differences in growth made by *Bassia* when grown on *Halogeton* soil (right) or *Bassia* soil (left) about one month after seeds were sown into pots.

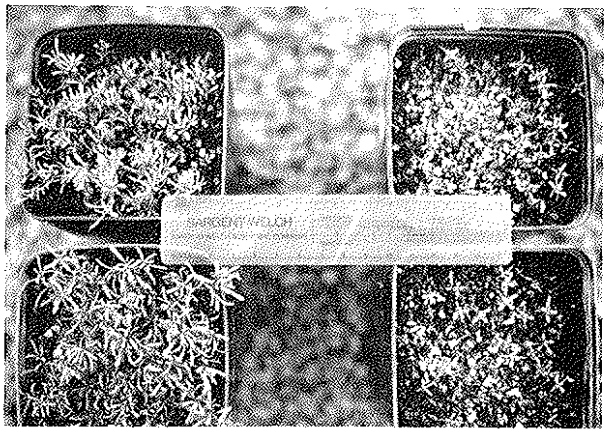


Figure 14. Photograph showing differences in growth made by *Halogeton* when grown on *Halogeton* soil (right) or *Bassia* soil (left) about one month after seeds were sown into pots.

Plants were harvested about three weeks later, as it seemed observable differences between treatment combinations were diminishing. Figures 15 and 16 summarize the results of this study for *Bassia* and *Halogeton*, respectively. It is apparent that higher soil moisture content enabled *Bassia* to make significantly greater growth, but there were no differences in production on the two soils. Thus, the condition observed in Figure 13, after one month's growth, disappeared within the next month. The greater growth of *Bassia* in mixed stands, as found in the previous experiment, is again present.

Figure 16 shows, for *Halogeton*, that there was little growth increase at higher soil moisture content, although the pure-stand *Halogeton* grown on *Bassia* soil showed a slight response. *Halogeton*'s response to the soils was significant inasmuch as pure-stand plants grown on *Bassia* soil grew more than those on *Halogeton* soil. The mixed pots did not show this and, in fact, had a uniform, and extremely low, biomass production. The much greater growth of *Bassia* than *Halogeton* is again evident here, but in this case the pure-stand plants on *Halogeton* soil didn't make any better growth than did those grown with *Bassia*; however, those in pure stands on *Bassia* soil were significantly more productive than the mixed-stand plants. Thus, the suppression of *Halogeton*'s growth by *Bassia* isn't as evident in this study as in the previous one. This may have been due to the shorter period of growth (57 vs. 119 days) here.

Table 13 contains results of the factorial analysis of variance on these data. It supports the major points evident from the figures, and also shows significant differences due to soils and the soils x species interaction; differences which are not as obvious from visual inspection. The significant interactions are pretty much to be expected, based on the main effect differences. The significant three-way interactions require more subtle interpretation and are not as important in a field context as are the other F-tests.

Seed Budget-Plant Demography Studies

Studies in this section deal with estimates of densities of seeds or plants at different life cycle stages during the study period. Their objective was to quantify seed-plant dynamics over a two-year period in order to assess the magnitude of vegetation change from one year to the next, and to quantitatively apportion annual seed production into use categories to determine the manner in which each year's seed production is dissipated. Seeds produced one year will either lie dormant in the soil, germinate, decay or be consumed the subsequent year. This study does not deal with seed decay or consumption but considers only dormant seeds and the fate of seeds which germinate.

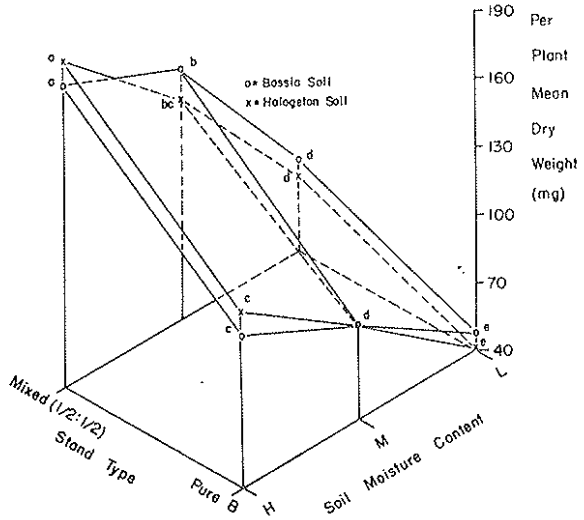


Figure 15. Mean dry weight (mg) of *Bassia* plants grown on two different soils, at three different soil moisture levels and in pure (36 *Bassia* plants per dm² pot) or mixed (18 *Bassia* and 18 *Halogeton* plants per dm² pot) stands. Field soil in which only *Bassia* grew represented by X points; in which only *Halogeton* grew, represented by O points (see Table 9 for soils data). Above-ground plant parts were harvested 57 days after seed was sown into pots. Soil moisture percentages (by weight) were: low = 12%; medium = 18%; high = 24%. n = 4 in all cases. Points with the same letter are not significantly different at the 95% confidence level, using Duncan's multiple range test.

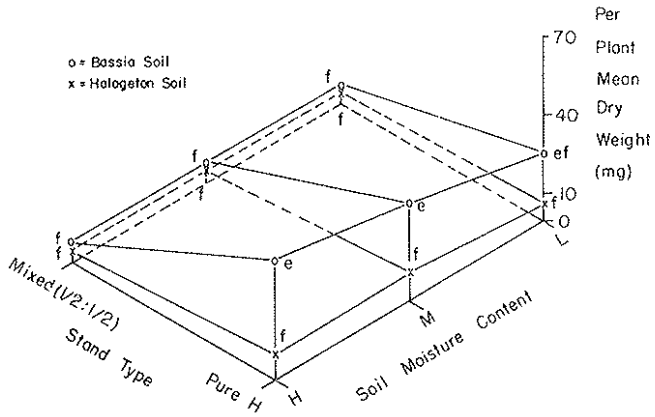


Figure 16. Mean dry weight (mg) of *Halogeton* plants grown on two different soils, at three different soil moisture levels and in pure (36 *Halogeton* plants per dm² pot) or mixed (18 *Bassia* and 18 *Halogeton* plants per dm² pot) stands. Field soil in which only *Bassia* grew represented by X points; field soil in which only *Halogeton* grew, represented by O points (see Table 9 for soils data). Above-ground plant parts were harvested 57 days after seed was sown into pots. Soil moisture percentages (by weight) were: low = 12%; medium = 18%; high = 24%. n = 4 in all cases. Points with the same letter are not significantly different at the 95% confidence level, using Duncan's multiple range test.

Table 13. Analysis of variance for mean plant dry weight comparing *Bassia* and *Halogeton* plants grown on two different soils, at three levels of soil moisture content and in pure or mixed (½:½) stands. There were four replicates per treatment combination and 36 plants per pot

Source of variation	Degrees of freedom	Mean squares	F value
Species (S)	1	.20	911.50***
Proportion (P)	1	8.44×10^{-3}	38.01***
Soils (So)	1	1.72×10^{-3}	7.79**
Water (W)	2	1.65×10^{-2}	74.18***
So x P	1	5.14×10^{-4}	2.32 n.s.
So x S	1	1.08×10^{-3}	4.86*
So x W	2	1.01×10^{-4}	.45 n.s.
P x S	1	2.97×10^{-2}	133.92***
P x W	2	3.14×10^{-4}	1.42 n.s.
S x W	2	1.28×10^{-2}	58.07***
So x P x S	1	1.32×10^{-3}	5.96*
So x P x W	2	7.33×10^{-5}	.33 n.s.
P x S x W	2	1.05×10^{-3}	4.75*
So x S x W	2	4.55×10^{-4}	2.05 n.s.
Error	74	2.22×10^{-4}	
Total	95	3.41×10^{-3}	

* = significant at the 95 percent confidence level.
** = significant at the 99 percent confidence level.
*** = significant at the 99.9 percent confidence level.
n.s. = not significant.

Soil Seed Reserves

A number of studies, usually in an agronomic context, have found very high numbers of viable seeds in soil, on the order of 10^4 to 10^5 per m^2, through the depth of the plowed layer (Brenchley and Warington 1930; Kropac 1966). The purpose of this investigation was to estimate numbers of hard (and therefore presumably viable, according to Stoller and Wax 1974) seeds in soil to a 3-cm depth in late June of 1974 and 1975. This time of year was chosen since it was after essentially all germination had taken place but before any newly produced seeds had fallen. Total annual seeds in soil are probably near their yearly low at this time and hence, represent ungerminated seed reserves.

Figure 17 summarizes these data on soil seed reserves by vegetation type for the different study sites in 1974 and 1975. Neither the bare site nor the open vegetation of the sage site was sampled in 1975 due to the excessive time required to process samples. It is evident that different sites have different densities of seeds in soil; the most pronounced change is that 1975 densities are noticeably lower than those in 1974. Only in the *Bassia* vegetation of the hill site were there more seeds in soil in 1975 than in 1974. The fence site shows the greatest change between years; 1975 densities are about one-seventh to one-eleventh as great as they were in 1974 for the *Bassia* and *Halogeton* vegetation types, respectively.

The only significant differences shown by analysis of variance of these data are the ones just mentioned for the fence site. There were no statistically significant differences between any of the other means, probably due to the high within-treatment variances. Major and Pyott (1966), in their review on buried viable seeds, state that point-to-point variability in numbers of seeds in soil makes statistically reliable sampling a practical impossibility. Further, they are wary of nonnormal data distributions since, in the field, seeds tend to aggregate about parent plants. My data were submitted to the W test for normality developed by Shapiro and Wilk (Dunn and Clark 1974) and were found to be normally distributed, an assumption important in parametric statistics.

Differences between sites within a year are to be expected due to variable amounts of seed production, but the generally lower 1975 densities are a more substantial result.

Figure 18 presents estimates of densities of seeds in soil by species on the study sites in 1974 and 1975. The "other" designation combines both *Descurainia* and *Lepidium* seeds. On all of the sites except sage, *Descurainia* was the major constituent in this category. For the hill, fence and sage sites, which contained two discrete types of vegetation, the seed densities have been computed based on the portion of the plot in which that species occurred. Roughly one-half of the fence site was dominated by *Bassia* and *Descurainia*, while the other half was dominated by *Halogeton*. Density of each species was computed based on total number of seeds recovered per unit area divided by the proportion of the plot in which that species occurred. This was considered to be the most realistic way to estimate density.

Coefficients of variation for the different species were on the order of 50 to 150%; because of this high variability, no statistical analyses were attempted. There are, however, several interesting aspects of these data. Nearly all of the species on each site had lower densities of seeds in 1975, with the fence site suffering greatest declines.

The "other" species, *Descurainia* and *Lepidium*, did not produce seed in 1974. Their lower 1975 values represent attrition due to germination, decay or consumption without seed reserve replenishment. On the hill site, the means indicate 24% of the "other" seeds were lost in one year; on the fence and sage sites, losses were 81 and 70%, respectively. Similarly, *Halogeton* produced no seed on the fence site in 1974 and its attrition rate over one year was 93%. Loss rates are likely related to species germination requirements; the drastic drop in numbers of *Halogeton* seeds seems to indicate that they germinate freely, as has already been related. Nearly all of the *Halogeton* seeds recovered were of the brown variety, which are nearly impossible to germinate under a variety of laboratory conditions; almost none of the easily germinable black seeds were recovered.

Summer Plant Establishment

The objective of the watering experiment carried on from mid-July to mid-September in 1974 was to see if there was a significant germinable reserve of seeds in the soil and to estimate its magnitude through counts of emergent seedlings. Very low numbers of plants emerged during the course of the watering treatment, and then only during the first few weeks after its initiation. The average number of plants emerging during the initial weeks was about one to two per each one-eighth m^2 quadrat.

These low rates of seedling emergence might be explained by insufficient amounts of water available for seed germination. The weekly addition of 25 mm equivalent of "rain" might not have raised soil water potential high enough for a long enough time to allow germination. No measurements were taken of soil water content in these plots but the soil surface was evidently damp for one to two days after water addition. In the first two weeks of September, the frequency of watering was increased to two 25-mm applications per week. There was no emergence in response to the increased water availability.

Another explanation for lack of emergence could be that seeds were dormant and would not germinate even with water abundantly available. The high temperatures of midsummer might be an environmental cue related to the dormancy-enforcing mechanism preventing germination. Whatever the reason for lack of emergence, data in the previous section indicate there were numerous viable seeds in the soil.

Seed Exclosures

An indication of the relative contribution to 1975 vegetation by 1974-produced seed and seed produced before 1974 is provided by results of the seed exclosure experiment. Areas of soil which were covered with cardboard boxes during the seed dispersal period in 1974 received no seed input. Comparable adjacent areas received a natural allotment of seed and differences between the covered and uncovered quadrats are an index to the impact of 1974 seed production, in terms of plants established in 1975.

Figure 19 summarizes these data from the covered and uncovered quadrats which had been watered during summer 1974. Data are presented for only three of the sites; densities on the fourth site (fence) were so near zero as to be not worth graphing. Each datum in the figure is the mean of 30 subsamples from 10 different quadrats, each quadrat containing three 1-dm^2 subsamples.

The graphs plainly show, for the initial sample date of May 26, that plant densities, on all sites, were much lower in the quadrats which had been covered during the seed dispersal period. The hill, sage and bare uncovered quadrats had 12.5, 28.5 and 14.9 times as many total plants established as the adjacent covered quadrats. This indicates that 1974 seed production generated the overwhelming majority of plants which became established in 1975. Correspondingly, 8, 4 and 7% of plants growing on the hill, sage and bare sites can be attributed to seed produced prior to 1974. Seeds of these species seem to have a short residence time in soil. Supporting this idea, the bare area, which had lowest seed production in 1974, also had lowest plant density in 1975.

There are evident differences in initial plant density between the three study sites. Density on May 26 for the covered quadrats ranged from a low of 10 *Halogeton* plants per m^2 on the sage site to a high of 177 *Bassia* plants on the hill site. The uncovered quadrats show greater absolute differences in densities, ranging from about 350 *Halogeton* plants per m^2 on the sage site to over 2300 *Bassia* or *Halogeton* plants on the hill site. These differences in density are probably related to numbers of seeds in soil available for germination and the favorableness of germination-establishment conditions on each site.

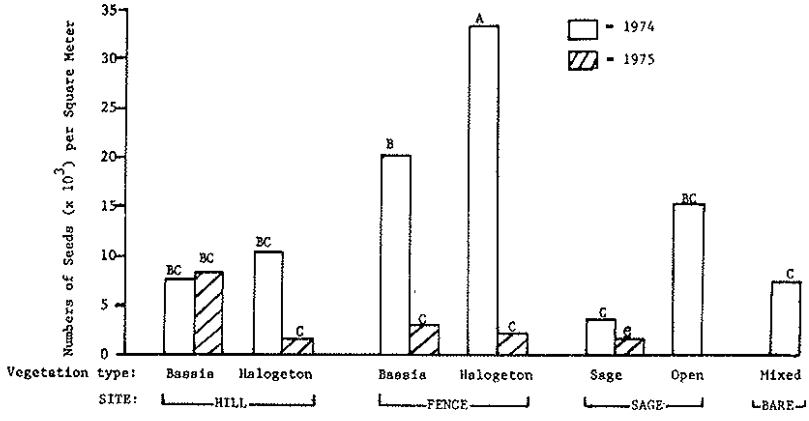


Figure 17. Numbers of hard seeds per square meter to a 3-cm depth on the various study sites in 1974 and 1975. For 1974 estimates, n = 10; for 1975 estimates, n = 7. Columns with different letters above are significantly different at the 95% confidence level using Duncan's multiple range test.

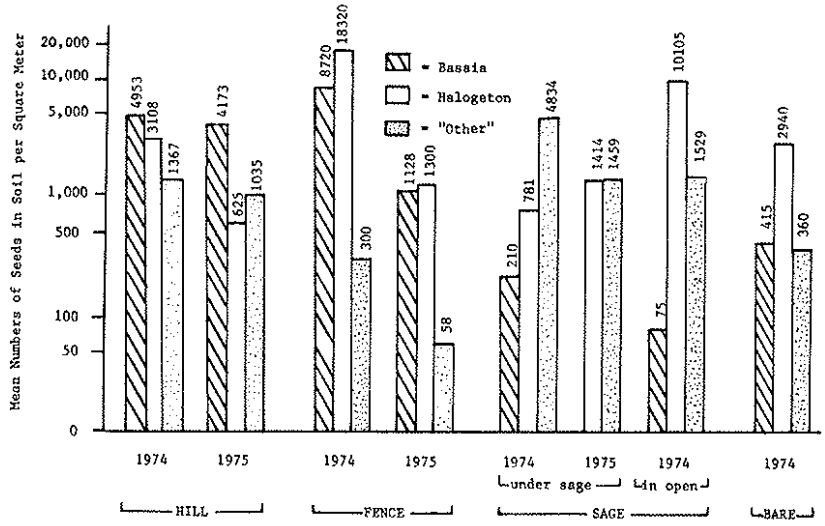


Figure 18. Mean numbers of seeds per square meter recovered from soil samples to a 3-cm depth on the different study sites in 1974 and 1975. Numbers atop the columns are densities for that group. Species lumped in the "other" category are *Descurainia pinnata* and *Lepidium perfoliatum*. Means are based on 20 samples for 1974 or 14 samples for 1975, except for the 1975 sage site which had 7 samples.

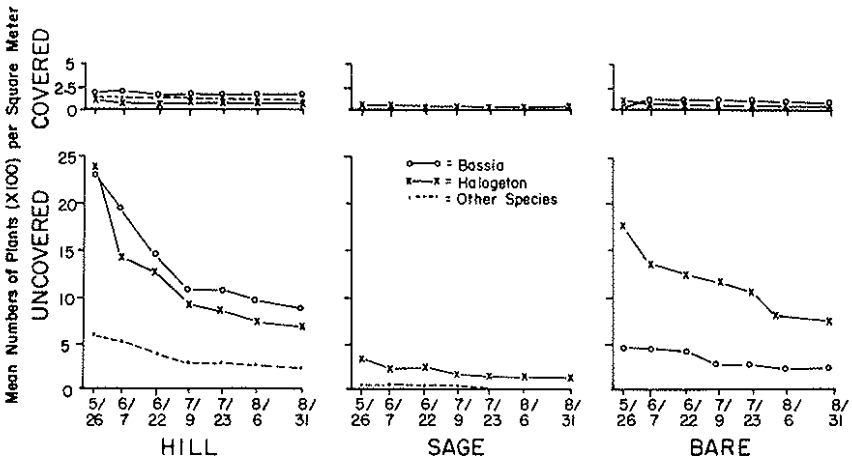


Figure 19. Mean numbers of plants (x 100) per square meter growing in 1975 in areas which had been either covered (preventing seed input) or uncovered (allowing seed input) during the seed dispersal periods in 1974. Each datum is the mean of 30 1-dm² subsamples, three subsamples taken from each of 10 quadrats.

Table 14. Overall mean densities of *Bassia* and *Halogeton* plants per square meter at the beginning and end of summer in 1974 and 1975 at permanent plots. Quadrats were 1 dm^2. There were 30 quadrats sampled on three of the sites; the hill site had 35 samples

Site	1974 Bassia	1974 Halogeton	1974 Percent Survival	1975 Bassia	1975 Halogeton	1975 Percent Survival	F Species	F Year	F Species x Year
HILL									
June	717	1063		1160	1083		.14	.42	.35
September	320	323	36	428	574	45	.34	2.01	.32
FENCE									
June	1973	1447		63	3		.95	31.06**	.60
September	180	0	5	53	3	85	6.27*	1.80	2.00
SAGE									
June	70	473		0	780		8.38*	.33	.85
September	0	63	12	0	357	46	6.55*	3.20	3.20
BARE									
June	493	596		547	583		.13	.01	.03
September	77	77	14	203	323	47	.68	6.58*	.68

* = significantly different at the 97.5 percent confidence level.
** = significantly different at the 99.9 percent confidence level.

During the summer growing season the covered and uncovered quadrats had significantly different numbers of plant deaths. There was little mortality in the quadrats which had been covered, due, presumably, to their initially low densities. Plants growing in the uncovered quadrats showed substantial density declines; in the early part of the summer the more dense stands (as on the hill site) thinned more rapidly. In July and August, the death rate generally diminished, indicating that plants surviving to this point had a greater likelihood of maturing.

Results of analysis of variance of these data support the major points just related. For each time period there were significant differences ($P < .01$) in density due to the exclosure treatment, and due to the three study sites. The exclosure x site interaction term was also significant ($P < .01$) indicating that the density response to the covered and uncovered treatments was not the same on the three sites.

Temporal Changes in Vegetation

Twice in 1974, in mid-June and mid-September, and six times in 1975 between May 25 and August 31, density counts were made at the permanent plots which had been spaced in a 5 x 5 m grid of the four study sites. These counts provide documentation of changes in vegetation between a dry and wet year (1974, 1975) and, for 1975, the pattern of postestablishment mortality.

Year-to-year changes—Density estimates made near the beginning and end of summer in both years are presented in Table 14 along with F values from analysis of variance done between years for each site on these density estimates. The beginning sampling dates were June 25, 1974, and June 22, 1975; the ending dates were September 4, 1974, and August 31, 1975. Though the dates are not exactly one year apart, they are close.

The four sites exhibit different degrees of change within and between years. The hill site was the most stable, showing no significant differences in density of *Bassia* or *Halogeton* at the beginning and end of either year. In contrast, the fence site was quite changeable; it had high densities of both species in June of 1974 and very low densities in June of 1975, hence the significant difference between years. By September of 1974, all the *Halogeton* had died, and it remained essentially absent through 1975; thus, there was a statistically significant difference in density of the two species in September which had not been present in June.

The sage site shows no significant difference between years but there is a significant difference in species due to *Bassia*'s near absence. The year and species x year interaction F values approach significance (F at $P = 0.05$ is 3.92) for the September date due to the relatively higher *Halogeton* density in 1975 and *Bassia*'s continued absence. The bare site showed a significant difference in density in September of the two years; the wetter 1975 conditions allowing more plants to survive.

Comparing percent survival in the two years for each site, it was always greater in 1975, probably due to the higher rainfall.

Postestablishment mortality—The patterns of decline in density for *Bassia* and *Halogeton* on three of the study sites during the summer of 1975 are shown in Figure 20. It is evident that initial densities are highest on the hill site. Through June and July, plants on this site also had the most rapid rate of decline. In August, death rate was about the same for all of the sites. The three lower density lines (for bare and sage sites) generally had quite similar mortality through the summer.

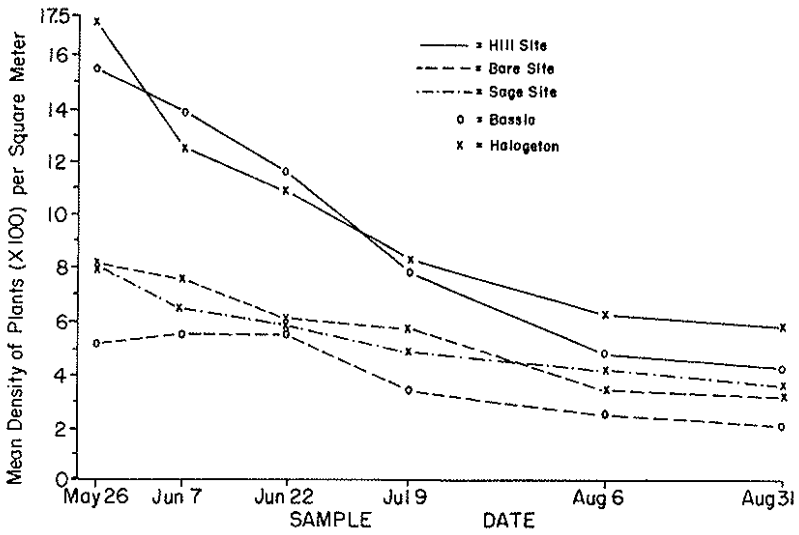


Figure 20. Mean numbers of *Bassia* (O) and *Halogeton* (X) plants per square meter on three different sites during summer 1975. n = 30 for sage and bare sites and 35 for hill site.

These data were submitted to statistical analysis comparing initial and final numbers of plants present between sample dates with the three sites and two plant species as treatments. This analysis showed that there were significant density differences ($P < .001$) between sites, due, no doubt, to the initially high densities on the hill site. There was no significant difference in density of *Bassia* or *Halogeton* on the sites, though.

The more interesting next step in this analysis was to use covariance techniques to remove effects of initial density differences between treatments for each of the sample dates. After doing this, the significant difference between sites, described above, disappears. This is an indication that changes in density between sample periods are dependent on the number of plants initially present. In fact, a regression analysis containing subsets for the species, the sites, the species x site interaction and the number of plants alive at the previous sample period, showed only the final term to be significant ($F = 3767.65$)).

A regression of number of plants alive at one sample period against number of plants present at the previous sample period was highly significant ($F = 4068.18$) and had an r-square value of .90. The equation for this precisely predictive relationship was $Y = .8350 + .7571X$, where Y equals the density of live plants at one of the sample dates and X equals the number that were alive at the previous sample date. This equation does not provide an instantaneous mortality rate, but rather applies to the time periods between sample dates over the summer. The equation represents something of an average death rate, in that covariance removed effects of initial density differences between treatments, and all of the data were used in the analysis.

At the beginning and end of the growing season for these annuals, other factors such as temperature or relative air humidity might be more important predictors of mortality. However, during this summer growing period, by which time most plants have become well established or have already died due to abiotic stress, mortality is closely related to density. This highly density-dependent mortality implies that competition for resources is keen between these plants, in that the number of deaths occurring in the next couple of weeks can be predicted quite well simply by knowing the numbers of plants now present.

Seed Production

The final bit of information necessary to produce a fairly complete picture of seed-plant dynamics through time was seed production in 1974 and 1975. These estimates were made using regression and dimensional analysis techniques. For *Bassia*, *Halogeton* and *Descurainia* lengths of flowering stalks, or fruits in *Descurainia*'s case, were measured and the numbers of seeds along that length were counted. These data were then used to generate a regression line for each species using a stepwise multiple regression program which predicted seed number based on inflorescence length, or a transformed variable of inflorescence length (A3UDD01).

For each species the equations are as follows:

Bassia:

$$Y = 11.97 + 1.368X,\ r^2 = .98,\ n = 66;$$

Halogeton:

$$Y = 3.891 + 1.796X,\ r^2 = .53,\ n = 115;$$

Descurainia:

$$Y = 9.519 + 8.901 \times 10^{-5} X^4,\ r^2 = .59,\ n = 140;$$

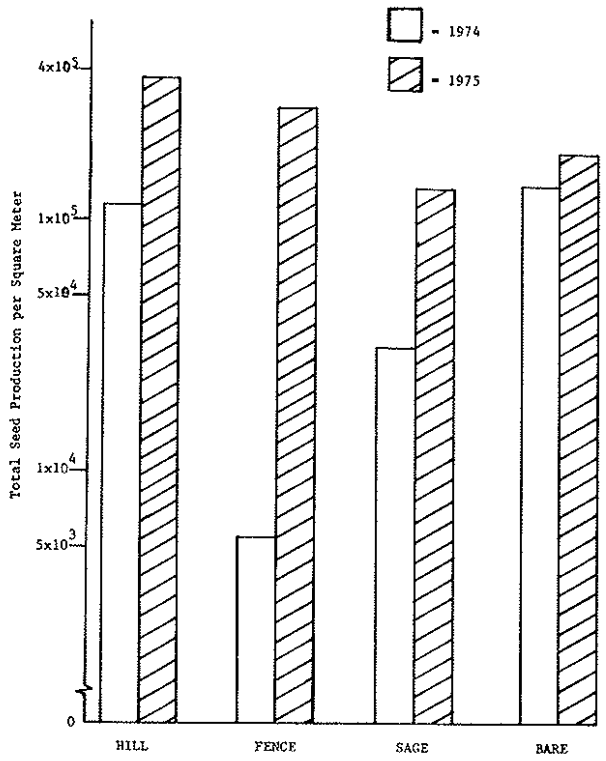


Figure 21. Total numbers of seeds produced per square meter on the study sites in 1974 and 1975.

where number of seeds is Y and length of fruit-bearing stalk is X. These regressions are all highly significant ($P < .01$) but the *Bassia* equation predicts with much narrower confidence limits. It was evident while measuring the *Halogeton* and *Descurainia* stalks that variability was quite high.

By collecting whole plants from the field, measuring lengths of all seed-bearing stalks and applying the regression equations to the data obtained, it was possible to make estimates of numbers of seeds produced per plant. In the process of collecting plants for measurement, a density estimate for each of the fruiting species was obtained. From these two measures, several estimates of seed production were generated.

Figure 21 presents data on the total numbers of seeds produced per m^2 by all species in 1974 and 1975 (A3UDD02). It is apparent that all sites had greater seed production in 1975 than in 1974. The bare site showed the least change between the two years; the 1975 amount of 1.88×10^5 seeds per m^2 was about 1.4 times more than the amount produced in 1974. The fence site showed a tremendous difference between the two years; about 52.5 times more seed was produced per m^2 here in 1975 than in 1974. Worth recalling here is the fact that most plants on this site died without producing seed in 1974.

With these weedy annuals, size and seed production per plant are indices of vigor. With this in mind, the data on per plant seed production presented in Figure 22 are informative, despite high variability (coefficients of variation ranged from 50 to 250%). *Descurainia* and *Lepidium* were absent in 1974, but in 1975 generally produced more seeds per plant than the *Bassia* or *Halogeton* they grew with; probably due to their early seed

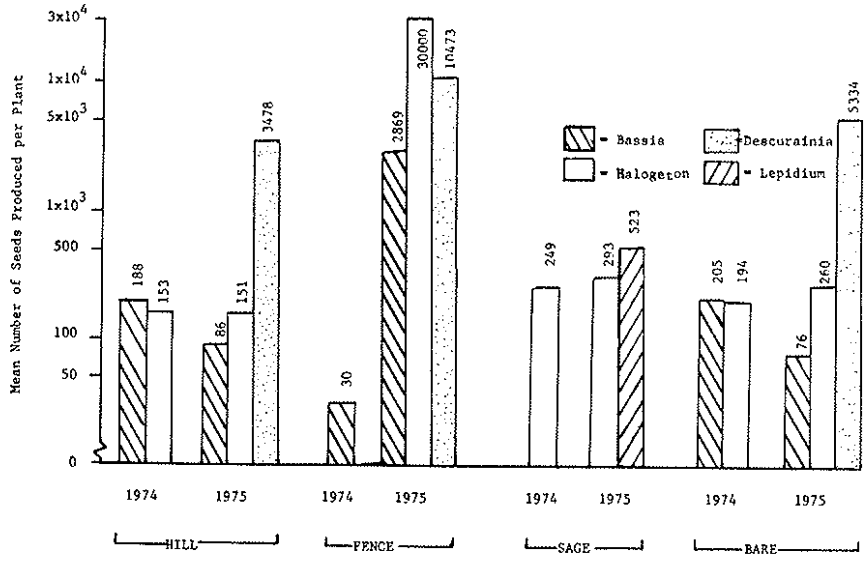


Figure 22. Mean number of seeds produced per plant by the different species growing in 1974 and 1975.

production, enabling them to utilize the more abundant May-June soil water. In turn, the *Bassia* plants which coexisted with *Descurainia* in 1975 on the hill and bare sites were smaller than in 1974. On these two sites, 1975 was a worse year for *Bassia* than 1974, even though rainfall was greater. A logical inference is that *Descurainia* usurped soil water from *Bassia*, causing it to be more stressed during summer 1975, and therefore less productive. Contrastingly, *Halogeton* shows little variation in seed production per plant between the two years, except on the fence site.

The story on the fence site is again one of drastic change between the two years; only small *Bassia* plants in 1974, but in 1975 the plants were very large. This is due to the very low densities of plants here, interplant distances were great -- often a meter or two -- and the high growth potential of individuals was realized.

Figure 23 converts per plant seed production to a density basis, computed over the area in which the various species occurred. The most striking thing is the tremendous density of seed production by *Descurainia* on the hill site -- nearly 650,000 seeds per m^2 from this dense stand. *Bassia* again shows lower densities of seed production on the hill and bare sites, while *Halogeton* shows higher densities. The increase by *Halogeton* isn't due to differences in plant size, but rather higher plant densities (Table 14). The fence site, despite its huge plants, did not have tremendously high densities of seed production due to the low plant densities.

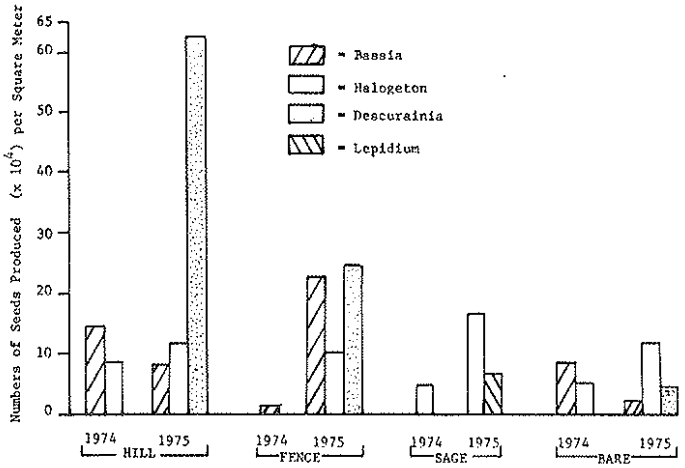


Figure 23. Mean numbers of seeds produced in 1974 and 1975 by species for the four study sites.

DISCUSSION

Dispersal, Establishment and Competitive Exclusion

The data from Figures 1, 2, 3 and 4 on numbers of seeds in soil across the *Bassia-Halogeton* ecotones, seed dispersal and seed germinability, collectively indicate that reasonable numbers of seeds disperse across the ecotone and germinate in the adjacent monospecific stand. The fairly restricted seed dispersal results in the majority of seeds being deposited near parent plants but the small percentage contaminating the adjacent vegetation should be a nucleus for mutual invasion of the pure stands.

The data in Figure 1 on seeds in soil imply that seeds of the absent species haven't accumulated in the adjacent vegetation, since the below-ground seed population reflects the above-ground vegetation composition. The field and lab germination studies corroborate this by demonstrating little difference in the germination behavior of *Bassia* or *Halogeton*. This evidence seems fairly strong; that dispersal and germination are not the life cycle stages during which selection restricts the distribution of *Bassia* or *Halogeton* on these study sites.

The next group of experiments on success of seedling establishment, drought tolerance of the two species and differences in soils, provide substantial evidence toward explanation of the adjacent pure stands of *Bassia* and *Halogeton*.

The average establishment rate (8%) for the seeds sown onto the soil indicates few seeds become plants. Sharitz and McCormick (1973) also found that for the two pioneer annual species which had concave survivorship curves a great deal of mortality occurred at the seedling stage. Harper (1965) states that environmental tolerance ranges in early stages of plant growth are often very much narrower than what adult plants can withstand. This definitely is the case here as preestablishment mortality was so much greater than growing season (postestablishment) mortality. Data from Table 7 indicate that of the 8% of sown seeds which were established in May, 54% died during the growing season. Thus, approximately 92% of seeds died by May 16, an additional 46% died during summer, leaving about 4% of sown seed as reproducing plants.

Seedling establishment success was markedly different in the various vegetation types as 1.8 times more *Halogeton* plants became established than *Bassia* (Fig. 5). Physiological differences between the species coupled with heterogeneous soil surface conditions probably account for much of the differential establishment success. The obvious differences in soil chemistry shown in Table 9 reinforce the inference that *Bassia* cannot establish as well on more extreme sites, while *Halogeton* can. From results of the drought-tolerance experiment (Table 8), it can be inferred that since young *Bassia* plants (4-5 weeks) are less drought-tolerant than those of *Halogeton*, comparable seedlings in the field might be similarly less tolerant and therefore be restricted to more mesic sites.

There can, however, be year-to-year differences in degree of establishment success. A very mild spring might allow *Bassia* to colonize areas generally dominated by *Halogeton*. The growth chamber study using the two different soils showed that, after initial repression of both species on *Halogeton* soil (establishment phase), there were no drastic

differences in production on the two soils after 57-days growth. Extrapolating this to the field situation, a mild spring might provide an opportunity for *Bassia* to invade areas which can generally be colonized only by *Halogeton*. With successful reproduction, the successional trend in one or more areas might be shifted.

So, to summarize, it seems the establishment phase is critical in determining vegetation composition from one year to the next, since so much mortality takes place at this stage. *Bassia* and *Halogeton* have considerably different requirements for successful establishment; *Bassia* is restricted to relatively mesic microsites but *Halogeton* can establish under very severe conditions.

Competition Experiments

The results of the three experiments on competition seemed somewhat contradictory, as watered *Halogeton* plants in the field became much larger (Fig. 9) than *Bassia* plants, but in the two growth chamber studies, *Bassia* grown in mixed stands far outstripped *Halogeton* (Figs. 11, 12, 15 and 16).

Both growth chamber studies can be characterized by wet initial growth conditions and harvest after a shorter period, relative to the field experiment. Under these more mesic conditions, *Bassia* was the aggressor, able to exploit more than its "share" of the factors of the environment.

In the field, however, *Bassia* did not respond to summer moisture additions but *Halogeton* did. Although there was no initial difference in weight of plant tops (Fig. 9), *Halogeton's* greater drought tolerance may have allowed it to make more root growth early in the growing season. This might have enabled it to monopolize the added water and account for *Bassia's* unresponsiveness.

The suppression of *Halogeton* by *Bassia* in the first (timing-proportion) growth chamber study is evident due to *Halogeton's* diminished production in mixed stand, relative to the pure stand (Figs. 11 and 12). Pure-stand pots containing *Halogeton* were significantly more productive in this experiment than *Bassia*-containing pots. Along the same lines, in the second growth chamber study at low water availability (Figs. 15 and 16), and in the control treatment for the drought-tolerance experiment (Table 8), there were no significant differences in biomass for the two species grown in pure stands.

In the soil-watering levels study, *Halogeton* was not nearly as responsive to increasing water availability as was *Bassia* (Figs. 15 and 16). This may have been due to the fact that only biomass of plant shoots was measured.

In these experiments it is difficult to say what the specific limiting factor for growth is, and why one species grows more rapidly than the other under certain conditions. There seemed to be no evidence of competition for light, as neither species creates a dense canopy. Determining competitive ability for soil growth resources is difficult to do.

Synthesis

The adjacent *Bassia* and *Halogeton* pure stands can be explained based on fairly restricted seed dispersal, differential establishment success due to dissimilar soil conditions, drought tolerance and competitive interactions. The fairly restricted seed dispersal results in a low percentage of seeds of the invading species entering the neighboring vegetation. Microsite differences allowed significantly more establishment success of one species than the other on nearly all of the sites (Fig. 5). The severe selection at this stage results in the two species being mostly confined to areas where they are likely to reproduce successfully. *Halogeton's* establishment success was 1.8 times that of *Bassia*, but growing-season mortality percentage was nearly the same (Table 7) for both species, since selection during establishment had already confined the species to sites more favorable for their growth habits.

The drought tolerance and competition experiments demonstrated differential responses of the species to changing degrees of physical and biotic stress factors. *Halogeton's* succulent tissues enable it to survive drought, but it is not as well able to respond rapidly to freely available moisture as *Bassia*.

The abruptness of the ecotone between the communities may be partly attributed to an abrupt change in soil parameters, but, more important, may be modification of soil surface properties by both species. The species may tend to accentuate the "tension zone" bounding them. *Bassia* litter enhances soil surface properties pertinent to its establishment by decomposing slowly and becoming incorporated into the surface soil. The sodium-accumulating *Halogeton* litter decomposes rapidly, causing deterioration of soil surface properties, so that eventually it is about the only species which can become established on these sites.

Plant Demography-Seed Budget Studies

Despite 90% spring mortality, dense stands of vegetation were present in May and June of both study years. Tables 1 and 2 indicate that densities ranged from about 70 plants to over 1500 plants per m^2, with the mean at about 800. Densities of seedlings on California annual ranges as reported by Evans et al. (1975) and Biswell and Graham (1956) are considerably higher than this -- on the order of 50,000 per m^2 -- as a maximum. Beatley (1967) found only one to three native annual plants per m^2 on several different areas of the Nevada Test Site in the Mohave Desert in 1963. Annual plant densities can vary tremendously from year to year and regionally.

Seed Production

The critical event influencing composition of these annual plant communities, regardless of how many plants establish and survive, is seed production. With annuals, the plant can be thought of as the means whereby a seed produces more seeds; the species most successful at this task should eventually gain dominance of a site. Sharitz and

McCormick (1973) call per plant seed production reproductive potential. Total seed production per unit area is somewhat independent of plant density, particularly with these weedy annuals; a single individual may produce one seed or upwards of 30,000. In this study it was evident (Fig. 22) that per plant seed production was extremely variable, but also quite high.

There are some trends evident in Figures 22 and 23 on seed production which can be extrapolated to infer the successional trend of the sites. In 1974, seed production per plant and per square meter were generally lower than in 1975. More favorable precipitation in 1975 allowed larger plants and more total seed production. The important thing, though, is that on two of the three sites in which it occurred in 1975, *Descurainia* produced a higher density of seeds than the other species. It probably also caused *Bassia*'s seed production to be diminished over what it might have been by cohabiting the sites favored by *Bassia* and usurping soil moisture. The expectation would be, confirmed by observations in 1976, that *Descurainia*'s dominance of the site would increase. The principles first hypothesized by Piemeisel (1951), that earlier-maturing species would displace the late-maturing initial occupants by usurping soil water, definitely apply here. The data on seed production support Piemeisel's hypothesis.

Soil Seed Reserves

Seeds of these species fall freely from the plant at maturity and come to rest at different locations near the soil surface where they may remain for variable lengths of time, dependent on their germination requirements, how favorable the microsite is for germination, the likelihood of consumption by rodents and several other parameters.

Results of this study indicated a very low carryover of soil seeds across more than one growing season. Production of 1975 vegetation was highly dependent on 1974 seed production. The data from seed exclosures, presented in Figure 19, indicate only about 6% of plants established in May 1975 were generated from seed produced prior to 1974. The fence site, which had almost no seed production in 1974, had very low plant densities in 1975 (Table 1). These results indicate a considerable instability in density of vegetation from one year to the next due to the dependence of plant production on seed produced the previous year.

This hypothesis is also supported by soil seed reserve estimates (Fig. 17). The 1975 densities were about 25% of the 1974 densities. This 75% decrease occurred in spite of generally "reasonable" amounts of seed production in 1974. The loss rate of seeds from the top 3 cm of soil here is even more rapid than that observed by Roberts and Feast (1972, 1973). Their comparable, uncultivated treatment indicated about 37% emergence and 12% viability loss for a total decrease of 49% in soil seed numbers over one year. My results showed a 75% mean decrease over one year in spite of 1974 seed production. Losses of seed to rodents may have been considerable, though.

This rapid turnover rate of seeds in the upper 3 cm of soil is likely due to a high germination percentage in the spring. The studies on seed germination (Figs. 3 and 4, Table 5) indicated a high germination percentage of *Bassia* and black *Halogeton* seeds. The brown *Halogeton* seeds, which were almost the only variety found in the soil seed samples, definitely seem to be the more stable seed reserve, probably due to their more complex germination behavior (Cronin 1965). Due to lack of disturbance, it is unlikely that many seeds would become buried very deeply on this site, and the slow spring snowmelt with gradually warming temperatures seems likely to create very favorable germination conditions. Year-to-year climatic differences influence the portion of the total seed pool which germinates. Weather conditions in any one year may favor germination of one species more than another.

Seed Budget-Plant Plasticity

Combining the estimates of total seed production and total seed reserves for 1974 and 1975, a contrasting picture of seed-plant dynamics becomes evident for the fence and hill sites over the study period. Figures 24 and 25 present these synthesized data for the fence and hill sites, respectively. Seed production and germination and other losses of seeds have been represented as single events across the time scale. The inflowing arrows represent seed production from reproductive plants.

Starting with not greatly different densities of seeds in soil in summer 1974 (2.73×10^4 vs. 9.16×10^3 per m^2), the two sites have tremendously different amounts of seed production (5.5×10^3 vs. 1.15×10^5 seeds per square meter, fence and hill sites, respectively) at the end of the growing season since most plants on the fence site died. Thus, at the end of 1974, there were roughly 3.8 times more seeds available for germination in 1975 on the hill sites.

This indicates the importance of each year's seed crop to the level of soil seed reserves, since there is little carryover seed in soil relative to the amount which might be produced each year. Seed production on the hill site in 1974 was 12.5 times greater than the density of seeds in soil, while on the fence site it was only two-tenths of the number of reserve soil seeds. Similar comparisons of this sort can be made from Figures 17 and 21 on seed reserves and seed production. Seed production is roughly 10 to 20 times more than numbers of reserve seeds in soil.

The percent loss of soil seeds by the summer of 1975 was approximately the same for the two sites, a 92% loss on the fence site and a 96% loss on the hill site. The assumption here is that most of this loss was due to germination. Despite nearly equal percent losses, the absolute numbers lost per square meter were greatly different on the two sites: 3.03×10^4 on the fence site and 1.19×10^5 on the hill site. Roughly 3.9 times more seeds were lost from soil on the hill site. As a result, many more plants were established on this site in May 1975 (Table 1).

Since 1975 was a fairly favorable precipitation year, the

few plants established on the fence site did very well, and, due to their plasticity and tremendous growth potential, became very large. Contrastingly, on the hill site, plants growing in considerably denser stands suffered under a greater degree of competition, and consequently were much smaller than those on the fence site (Fig. 22). Despite these differences in plant size, seed production per unit area in 1975 was not greatly different on the two sites (Fig. 21). Figures 24 and 25 indicate that, at the end of the 1975 growing season, density of soil seeds on the fence site was 76% as great as on the hill site whereas, at the end of the 1974 season, they had been only 26% as great.

The near failure of the 1974 seed crop on the fence site affected density of the 1975 vegetation but, due to reduced competition and plant plasticity, the 1975 seed crop was nearly the same as on the hill site, which had a "normal" amount of seed production in 1974. Thus, plant plasticity served a homeostatic function on the fence site, resulting in a high amount of 1975 seed production which might not have been expected based on the number of plants growing on the site in the spring of 1975.

Plant size does have implications for the successional trend of a site. A single plant established on a low-density site can

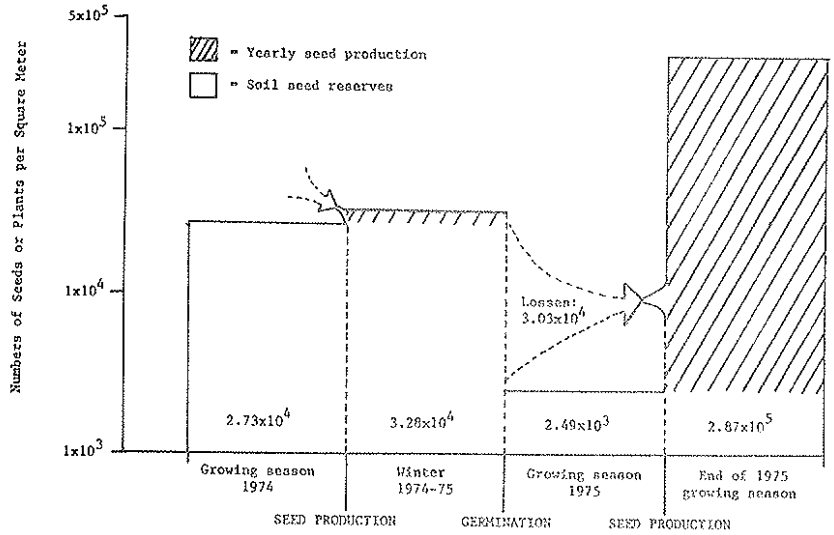


Figure 24. Seed budget for fence site. Combined estimates of soil seed reserves and seed production in 1974 and 1975. Inflowing dashed arrows represent seed production from reproductive plants. Shaded areas represent the portion of total seed reserves due to each year's seed production.

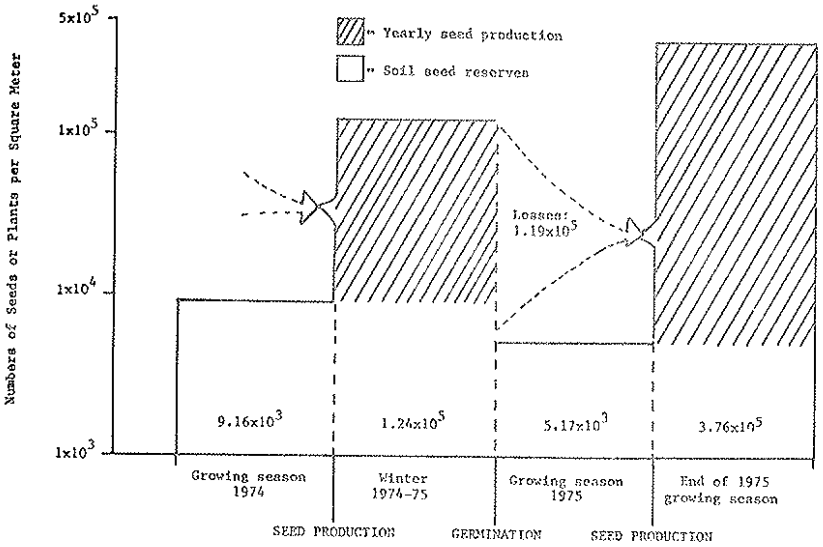


Figure 25. Seed budget for hill site. Combined estimates of soil seed reserves and seed production in 1974 and 1975. Inflowing dashed arrows represent seed production from reproductive plants. Shaded areas represent the portion of total seed reserves due to each year's seed production.

become very large and make a much greater proportionate contribution to the year's seed production than if it had been established on a high-density site. Its importance in the subsequent year's vegetation would likely be greater, due to its greater representation in the soil seed pool. Rate of vegetation change could be more rapid in low-density stands with large plants; the impact of a single invader could be much greater.

Plant size has an additional impact on site development through the manner in which litter is deposited. Small plants undergo decomposition more rapidly due to their smaller stem diameter and the fact that they more easily become pressed against the soil surface by winter snows. They more rapidly provide a positive increment of organic material to the soil surface, while large plants (many plants in 1975 were more than a meter tall and more than 40 cm in diameter) tend to remain erect, withholding their organic material above the soil.

One of the major factors controlling succession in these weedy communities is degree of microsite development, which mainly progressed by deposition of litter (Piemeisel 1951; Evans and Young 1970). Dense stands will generate uniform litter deposition while sparse stands with large plants will produce islands of shade and litter. Plants growing in 1976 on the fence site under remnants of the large 1975 plants were observed to be significantly larger and more vigorous than those growing in more exposed locations.

LITERATURE CITED

Balph, D. F. (coordinator) et al. 1973. Curlew Valley Validation Site report. US/IBP Desert Biome Res. Memo. 73-1. Utah State Univ., Logan. 336 pp.

Beatley, J. C. 1967. Survival of winter annuals in the northern Mojave Desert. Ecology 48:745-750.

Biggs, W. W., A. R. Edison, J. D. Eastin, K. W. Brown, J. W. Maranville, and M. D. Clegg. 1971. Photosynthesis light sensor and meter. Ecology 52:125-131.

Biswell, H. H., and C. A. Graham. 1956. Plant counts and seed production on California annual type ranges. J. Range Manage. 9:116-118.

Blackburn, W. H., and C. M. Skau. 1974. Infiltration rates and sediment production of selected plant communities in Nevada. J. Range Manage. 27:476-480.

Brenchley, W. E., and K. Warington. 1930. The weed seed population of arable soil. I. Numerical estimation of viable seeds and observations on their natural dormancy. J. Ecol. 18:235-272.

Brown, R. W. 1970. Measurement of water potential with thermocouple psychrometers: construction and applications. USDA Forest Serv. Res. Paper INT-80. 27 pp.

Chaudhuri, I. I., and H. H. Wiebe. 1968. Influence of calcium pretreatment on wheat germination in saline media. Plant and Soil 28:208-216.

Cronin, E. H. 1965. Ecological and physiological factors influencing chemical control of *Halogeton glomeratus*. USDA Tech Bull. 1325. 65 pp.

Cronin, E. H. 1973. Pregermination treatment of black seed of *Halogeton*. Weed Sci. 21:125-127.

deWit, C. T. 1960. On competition. Versl. Landbouwk. Onderz. 66:1-82.

Dunn, O. J., and V. A. Clark. 1974. Applied statistics: analysis of variance and regression. John Wiley and Sons, New York. 387 pp.

Evans, R. A., B. L. Kay, and J. A. Young. 1975. Microenvironment of a dynamic annual community in relation to range improvement. Hilgardia 43:79-102.

Evans, R. A., and J. A. Young. 1970. Plant litter and establishment of alien annual weed species in rangeland communities. Weed Sci. 18:697-703.

Friedman, J., and G. Orshan. 1975. The distribution, emergence, and survival of seedlings of *Artemisia herba-alba* in the Negev Desert of Israel. J. Ecol. 63:627-632.

Harper, J. L. 1960. Factors controlling plant numbers. Pages 119-132 *in* The biology of weeds. Symp. Brit. Ecol. Soc. Blackwell Sci. Publ., Oxford.

Harper, J. L. 1961. Appproaches to the study of plant competition. Pages 1-39 *in* Mechanisms in biological competition. Symp. Soc. Exp. Biol. Academic Press, New York.

Harper, J. L. 1965. Establishment, aggression, and cohabitation in weedy species. Pages 243-268 *in* H. G. Baker and G. L. Stebbins, eds. The genetics of colonizing species. Academic Press, New York.

Harper, J. L. 1967. A Darwinian approach to plant ecology. J. Ecol. 55:247-270.

Hausenbuiller, R. L. 1972. Soil science principles and practices. William C. Brown Co., Dubuque, Iowa. 504 pp.

Hugie, V. K., and H. B. Passey. 1964. Soil surface patterns of some semiarid soils in northern Utah, southern Idaho, and northeastern Nevada. Soil Sci. Soc. Amer. Proc. 28:786-792.

Kinsinger, F. E., and R. E. Eckert, Jr. 1961. Emergence and growth of annual and perennial grasses and forbs in soils altered by *Halogeton* leachate. J. Range Manage. 14:194-197.

KNIPE, O. D., and H. W. SPRINGFIELD. 1972. Germinable alkali sacaton seed content of soil in the Rio Puerco Basin, west central New Mexico. Ecology 53:965-968.

KROPAC, Z. 1966. Estimation of weed seeds in arable soils. Pedobiologia, Jena, 6:105-128.

MAJOR, J., and W. T. PYOTT. 1966. Buried viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. Vegetatio Acta Geobot. 13:253-282.

PARMAR, M. T., and R. P. MOORE. 1966. Effects of simulated drought by polyethylene glycol solutions on corn (*Zea mays* L.) germination and seedling development. Agron. J. 58:391-392.

PEMADASA, M. A., and P. H. LOVELL. 1974. Factors affecting the distribution of some annuals in the dune system at Aberffraw, Anglesey. J. Ecol. 62:403-416.

PIEMEISEL, R. L. 1951. Causes affecting change and rate of change in a vegetation of annuals in Idaho. Ecology 32:53-72.

ROBERTS, H. A., and P. M. FEAST. 1972. Fate of seeds of some annual weeds in different depths of cultivated soil. Weed Res. 12:316-324.

ROBERTS, H. A., and P. M. FEAST. 1973. Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. J. Appl. Ecol. 10:133-143.

SHARITZ, R. R., and J. F. MCCORMICK. 1973. Population dynamics of two competing annual plant species. Ecology 54:723-740.

STOLLER, E. W., and L. M. WAX. 1974. Dormancy changes and fate of some annual weed seeds in the soil. Weed Sci. 22:151-155.

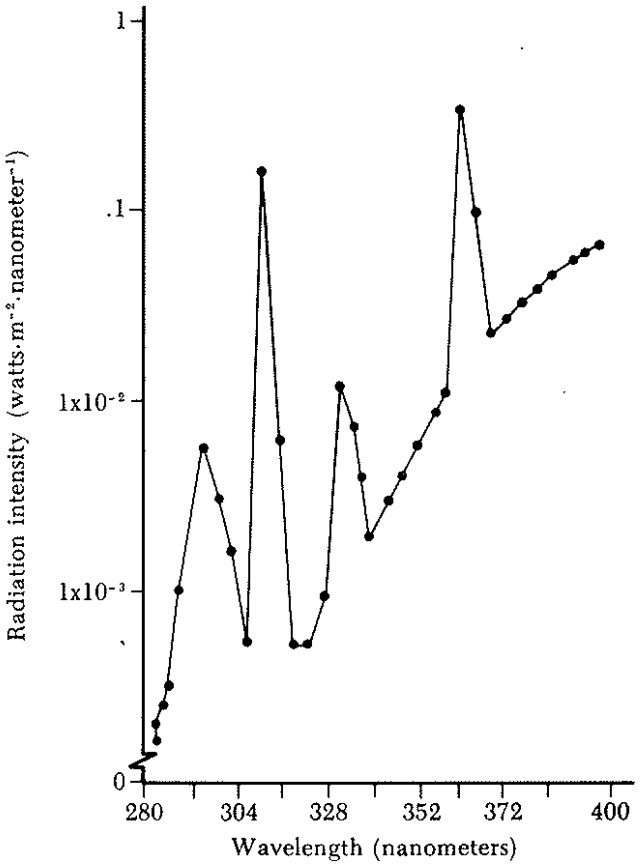
WERNER, P. A. 1975. A seed trap for determining patterns of seed deposition in terrestrial plants. Can. J. Bot. 53:810-813.

WOOD, M. K., R. W. KNIGHT, and J. A. YOUNG. 1976. Spiny hopsage germination. J. Range Manage. 29:53-56.

YOUNG, J. A., R. A. EVANS, R. O. GIFFORD, and R. E. ECKERT, JR. 1968. Germination of medusahead in response to osmotic stress. Weed Sci. 16:364-368.

APPENDIX I

SPECTRUM OF RADIATION INTENSITY IN THE SHERER-GILLETTE GROWTH CHAMBER IN THE ULTRAVIOLET RANGE FROM 280-400 NANOMETERS



APPENDIX II

SOIL PROFILE

Horizon	Thickness	Description
		Bassia Vegetation
O_1	.5-0 cm	Plant litter, decomposing organic material.
A_1	0-6 cm	Light brownish gray (2.5Y6/2) silt loam, dark brown (10YR3/3) moist; moderate fine subangular blocky structure, breaking to moderate, fine granular; soft, very friable, slightly sticky, plastic; abundant fine roots, incorporation of plant debris, moderately calcareous with many small vesicular pores 1-2 mm diameter.
B_2	6-30 cm	Light brownish gray (2.5Y6/2) silt loam, brown (10YR4/3) moist; weak, very fine platy structure breaking to moderate, fine granular; slightly hard, friable, slightly sticky, plastic; frequent fine roots, moderately calcareous, occasional fine (1-2 mm) pores.
C_{ca}	30-60 cm	Light gray (2.5Y7/2) heavy silt loam, grayish brown (2.5Y5/2) moist; moderate medium subangular blocky structure; hard, firm, sticky, plastic; occasional roots, few pores, extremely calcareous.
		Halogeton Vegetation
A_1	0-3 cm	Light gray (10YR7/2) silt loam, grayish brown (10YR5/2) moist; moderate to weak fine platy structure; slightly hard, friable, slightly sticky and plastic; abundant coarse and fine roots, moderately calcareous, with abundant vesicular pores (1-3 mm diameter) interlayered between platy structure.
A_{12}	3-10 cm	Quite similar to above but more compact as the vesicular pores become much less frequent and finally are completely absent.
B_2	10-36 cm	Light gray (10YR7/2) silt loam, grayish brown (10YR5/2) moist; moderate coarse platy structure; hard, firm, slightly sticky and plastic; moderately calcareous, many roots.
C_{ca}	36-60 cm	White (10YR8/1) silt loam, yellowish brown (10YR5/4) moist; moderately medium subangular blocky structure; slightly hard, friable, slightly sticky, plastic; moderately calcareous, frequent roots.